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STUDIES IN ARTOCARPUS AND ALLIED GENERA, IV. A REVISION OF ARTOCARPUS SUBGENUS PSEUDOJACA *

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38. *Artocarpus lakoocha* Roxb. Fl. Ind. 3: 524. 1832, "*Lakoocha*"; Graham, Cat. Bombay Pl. 193. 1839; Wight, Ic. Ind. Or. 2: t. 681. 1843; Tréc. Ann. Sci. Nat. Bot. III. 8: 117. 1847; Dalz. & Gibson, Bombay Fl. 244. 1861; Brandis, For. Fl. N.-W. & C. Ind. 426. 1874, pro max. parte; Kurz, For. Fl. Burma 2: 433. 1877; King in Hook f. Fl. Brit. Ind. 5: 543. 1888, pro parte; King, Ann. Bot. Gard. Calcutta 2: 14. 1889, p.p., quoad t. 13, excl. spec. *Griffith 4666*, *Main-gay 1479*; Renner, Bot. Jahrb. 39: 370. 1907; Kanjilal, For. Fl. Siwalik & Jaunsar, 379. 1911; Duthie, Fl. Upper Gang. Plain 3: 141. 1915; Troup, Silvicult. Ind. Trees 3: 883. fig. 326. 1921; Parkinson, For. Fl. Andaman Is. 253. 1923; Haines, Bot. Bihar & Orissa 5: 824. 1924; Parker, For. Fl. Punjab ed. 2. 487. 1924; Osmaston, For. Fl. Kumaon, 504. 1927; Fischer in Gamble, Fl. Madras 3: 1369. 1928, p.p., quoad spec. *Gamble et Lushington*; Parker & Singh, Common Indian Trees, 26. t. 20. 1933; Kanjilal et al. Fl. Assam 4: 268. 1940; Benthall, Trees Calcutta, 401. 1946. Holotype(?), Bengal, *Roxburgh s.n.*, Sept. 1812 (BM).

Artocarpus lacucha Roxb. Hort. Beng. 66. 1814, nomen nudum.

Artocarpus bengalensis Roxb. ex Wall. Cat. no. 4655C. 1831, nomen nudum.

Artocarpus reticulata Heyne ex Wall. Cat. no. 4655D. 1831, nomen nudum.

Artocarpus mollis Wall. Cat. no. 4661. 1831, nomen nudum.

Artocarpus yunnanensis H. H. Hu, Bull. Fan Inst. Biol. Peking Bot. 8: 32. 1937. Holotype, Yunnan, *Wang 77078* (PE, not seen); isotype (A).

Artocarpus ficifolia W. T. Wang, Acta Phytotax. Sin. 6: 274. t. 15, fig. 23. 1957. Holotype, Yunnan, *Exped. Biol. Sino-ross. ad prov. Yunnan 676* (PE ?, not seen); isotype (A).

Deciduous trees, height to 20 m., bark rough, grey or brown. *Twigs* 3–6 mm. thick, shallowly rugose, densely pubescent, hairs yellow to rufous, patent or subappressed, straight. *Leaves* 13–37 × 6–21 cm., elliptic, oblong or ovate, short-acuminate, base broadly cuneate, rounded or

* Continued from volume XLI, p. 109.

subcordate, often oblique, margin entire or denticulate towards the apex; juvenile leaves shallowly pinnatifid; main veins and reticulum prominent beneath, the areolae often slightly bullate; glabrous or nearly so above, venation beneath pubescent, hairs colourless to pale rufous, undulate; lateral veins 9–18 pairs, straight or curved; intercostals parallel; green, drying greyish, greenish or pale brown, venation straw-coloured, smallest meshes of reticulum nigrescent; petiole (10–)15–45 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 12–25 × (7–)10–18 mm., ellipsoid, obovoid or clavate; perianths of 2(or 3) free segments, 0.5 mm. long; stamen 0.9 mm. long, filament tapering above, anther-cells ellipsoid, 0.15 mm. long; bracts rather stoutly stalked, heads peltate, to 0.5 mm. across, these and perianths ciliate; peduncle 2–5 × 2 mm., short-pubescent; *female head* with styles exerted to 1–1.5 mm. through low papillae emerging between peltate bracts. *Syncarp* to 6 cm. across (to 12 cm. fide *Winit 301*), subglobose, shallowly lobed, yellow, drying brown, the surface irregularly papillate, pubescent, with numerous persistent bracts; walls c. 3 mm. thick; proximal region of perianths free, fruiting perianths several, fleshy, “seeds” (pericarps with a thin, horny endocarp) ellipsoid, 10 × 6 mm.; core c. 10 mm. across; peduncle 8–15(–25) × 4 mm., short-pubescent.

VERNACULAR NAMES: *lakuch* (Sanskrit), *barhal* (Hindi), *dahu* or *dheu* (Bengali), India; *myauklok*, Burma; *hat lom*, *hat non* (Lao), Siam. USES: the tree is often planted, especially in northern India, for its edible fruit.

DISTRIBUTION: in evergreen, semi-evergreen and moist deciduous forest to 6000 ft., in areas with a distinct dry season; eastern and northern India (Madras, Orissa and Bihar to Assam and Chittagong, and westward along the sub-Himalayan tract to East Punjab), Burma, Andaman Islands, Siam, Indochina, Yunnan; cultivated through much of its range and south to Bombay in India, sparingly introduced elsewhere in the tropics.

India. Not localized: “East India,” *Roxburgh* (κ, ♀); Himalaya, Tikoli Valley, *Edgeworth 216* (κ, ♂); Noholly, *Hooker f. & Thomson*, Dec. 1850 (κ, L, U, P); Punkabarry, *Gamble 1179A* (κ, ♂); Tenga Ghats, *sine nom.* 1204 (κ). EAST PUNJAB. Kangra, Bhadwar, *Koelz 4367* (A, ♂). HIMACHAL PRADESH. Lower Kanaor [= Kunawara], *Royle* (GH, P, ♀). UTTAR PRADESH. Kumaon: above Kota, *Strachey & Winterbottom* (GH, κ); Outer Hills, *Strachey & Winterbottom 18* (GH, κ, ♂). MADRAS. Ganjam District, Khalingia Ghat, *Gamble 13699* (κ); Vizagapatam, Rangalu Shola, *Lushington*, June 1914 (κ, ♀). BIHAR. Hazaribagh, *Meebold 3873* (κ, ♂, ♀); Singbhum, Karampoda forest, *Haines 636* (κ, ♀). ORISSA. Nilghiris, *Pierre 6* (P). Sikkim: *Hooker f.* (κ, ♀); below Kasseong, *Hooker f.*, Apr. 1850 (κ, ♂); Rangit River, *Clarke 27255* (κ), *King*, July 1876 (κ, ♀). BENGAL. *Roxburgh*, Sept. 1812 (BM, ♀), *Voigt* (C, ♂), *sine nom. et num.*, Dec. 1837 (L); Siligoree, *Clarke 11615B* (BM, ♀). ASSAM. Cachar, Luckhipoor, *Clarke 7018* (A); Haflong Hill, *Blatter 29156* (κ, ♀); Khasia Hills, *Hooker f. & Thomson* (c); Naga Hills, *Prain*, 1886 (CGE); Naga Hills, Lang,

Meebold 7156 (κ, ♂). MANIPUR. On the way to Chamoo [? = Tamu], *Watt* 5167 (CAL). CHITTAGONG. Hill Tracts, *King* 340 (SING, ♀), 417 (L, SING, ♂), *s.n.*, 1882 (L); *Khana, Hooker f. & Thomson* (κ).

Burma. Diamond Island, *Prain*, 30 Nov. 1889 (CAL); Myaungmya, *Labwuta, Lace* 2977 (κ, ♀); Phanac, fl. Saluan [? = Salween River], *Wallich* 4661 (CGE, κ, P, ♂, ♀); Rangoon *Buchanan Hamilton* (BM), *Dickason* 6947 (A, ♂); Rangoon, Kamayut, *Dickason* 8256 (A, ♂, ♀); Sandoway, near Taungup, *Lace* 2930 (κ, ♂). TENASSERIM. Amherst: Moulmein, *Falconer* 991 (L). Mergui: *Griffith* 1053 (κ, ♀). Andaman Islands. Ali Masfid Reserve, *Parkinson* 385 (κ, ♀); Baradang, *Parkinson* 205 (DD, ♂); Boru-Lung-Da, *Parkinson* 928 (DD, ♀). Siam. Dan Sai, Kao Keo Kang, *Kerr* 5804 (BM, ♂); Me Kok, Muang Fang, *Kerr* 5158 (BM, ♂); Me Lee, Lampoon, *Winit* 301, 302 (BM, ♂). PENINSULAR SIAM. Trang, Chawng, *Buncoed* 20 (CGE).

Indochina. LAOS. Pac Bac, near Luang Prabang, *Poilane* 20478 (P, ♀); between Phinh Ha and Lao Phu Tai, *Poilane* 25926 (P, ♂); Vientiane, *Poilane* 20782 (P, ♀). TONKIN. Lao Kay prov., between Nam Long and Phouy Tho, *Poilane* 25496 (P, ♂). China. YUNNAN. *Anderson*, 1875 (CAL), *Forrest* 12252 (κ, ♂); Chen-Kang Hsien, *Wang* 72645 (A, ♂); Chin-ping, Meng-la, *Exped. Biol. Sino-ross.* 676, Apr. 1956 (A, ♂); Fo-Hai, *Wang* 74902 (A, ♀), 77078, June 1936 (A, ♀); Lan-Tsang Hsien, *Wang* 76647 (A, ♀); Mienning, Nanya, *Yu* 18102 (A, ♂); Shunning, Hila, *Yu* 16805 (A, ♀); Szemao, *Henry* 11746 (A, κ, ♂, ♀).

The distribution of *Artocarpus lakoocha* has generally been given as India, Ceylon, Burma and Malaya, but three corrections to this must be made. Firstly, it was shown by Corner in 1939 (*Gard. Bull. Singapore* 10: 282) that the entity hitherto identified in Malaya as *A. lakoocha* in fact represented *A. dadah*, a species of western Malaysia. As already noted, the misidentification originated in King's description of this taxon as *A. lakoocha* var. *malayana*, which he did not distinguish satisfactorily from the type. His account of the latter is a mixture of the two species, but the plate was based on Roxburgh's original drawing of *A. lakoocha* (as was the plate in Wight's "Icones"). No collections of this species have been seen from farther south than peninsular Burma and Siam.

Secondly, it has been found that in India, also, two different taxa have been confused under the name *Artocarpus lakoocha*. This species appears to occur as an indigenous tree only in northern India and along the Eastern Ghats, although it is planted more widely. Several collections have been seen from the Bombay area, but none, apparently, is from a wild tree. This is supported by a statement by Graham in 1839 (the sole information traced in the literature) to the effect that *A. lakoocha* was only found in a cultivated state in Salsette and the North Concan. On the Western Ghats and in Ceylon there occurs another entity which has usually been identified as *A. lakoocha*. However, it has been found that it is quite distinct and it is described above as *A. gomezianus* ssp. *zeylanicus*, the differentiating characters being given there. *Artocarpus lakoocha* was described from Bengal and the type and drawing leave no doubt as to the application of Roxburgh's name. The references in which the two entities have been confused are indicated above as far as possible;

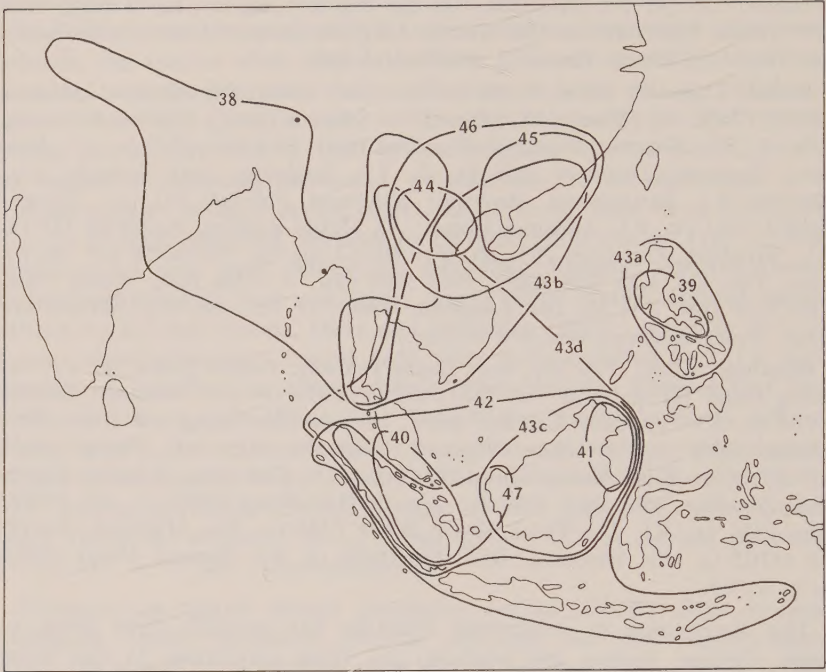


FIG. 19. Distribution of some species of subg. PSEUDOJACA. 38, *Artocarpus lakoocha*; 39, *A. rubrovenius*; 40, *A. fulvicortex*; 41, *A. tomentosulus*; 42, *A. glaucus*; 43, *A. nitidus*, a, ssp. *nitidus*, b, ssp. *lingnanensis*, c, ssp. *humilis* and ssp. *borneensis*, d, ssp. *griffithii*, dots, records not identified to subspecies; 44, *A. petelotii*; 45, *A. hypargyreus*; 46, *A. styracifolius*; 47, *A. altissimus*.

only those which were based primarily on *A. gomezianus* ssp. *zeylanicus* are cited under the latter.

Finally, the area of *Artocarpus lakoocha* must be extended eastward through Siam to Indochina, and to Yunnan from which it has been described twice without reference to Roxburgh. Most of the Indochinese collections were made after Gagnepain wrote up the Moraceae for the "Flore Générale de L'Indochine" (1928), and he did not mention *A. lakoocha*. The distinctions between this species and *A. tonkinensis* are given above, under the latter entity.

39. *Artocarpus rubrovenius* Warb. in Perkins, Frag. Fl. Philip. 166. 1905, "*rubrovenia*"; Merr. Philip. Jour. Sci. 1, Suppl. 43, 1906, Enum. Philip. Pl. 2: 43. 1923; Elmer, Leaf. Philip. Bot. 2: 622. 1909; Brown, Useful Pl. Philip. 1: 470. 1941. Holotype, Luzon, Warburg 12949 (B).

Trees, height to 15 m., bark mottled grey and brown. Twigs 2.5–5 mm. thick, appressed-puberulent, soon glabrescent. Leaves 11–26 × 5–14 cm., ovate to elliptic, with an acumen to 2.5 cm. long, base broadly rounded

to broadly cuneate, often oblique, glabrous, margin entire; main veins prominent beneath, intercostals slightly so; lateral veins 8-13 pairs, curved; intercostals parallel; green with yellowish-white main veins, drying brown or blue-grey above, paler brown beneath, venation reddish or nigrescent in young leaf, straw-coloured when mature; petiole 15-30 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 15-45 \times 10-20 mm., obovoid to clavate; perianths of 2-4 segments, free or fused at the base, 0.5 mm. long; stamen 0.7 mm. long, filament cylindrical, abruptly contracted above, anther-cells ellipsoid, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.3 mm. across, these and perianths pubescent; peduncle 1.5-3 \times 1.5 mm., velutinous; *female head* with styles exerted to 0.5-0.8 mm. through papillae emerging between peltate bracts. *Syncarp* (submature) to 3 cm. across, subglobose or shallowly lobed, drying brown or cinereous, the surface nearly smooth, short-pubescent, with numerous persistent bracts; proximal region of perianths free; peduncle 5-10 \times 3 mm., velutinous.

DISTRIBUTION: in forest to 1200 ft., Luzon (? also in Mindoro).

Philippine Islands. LUZON. *Haencke* 433 (NY, ♀). Quezon (Tayabas): Baler, Merrill 1034 (K, US, ♀), *Quisumbing* PNH 2511 (A, PNH, SING, ♀); Casiguran, Ramos & Edano BS 45226 (BO, NY, ♂); Lagumanoc, Merrill 2590 (K, US, ♂); Lucban, Elmer 9128 (A, BO, K, L, ♂), McGregor BS 47395 (NY, ♀); Sampolor, Warburg 12949, Mar. 1888 (B, ♂, ♀). Bataan: Curran 5439 (US); Lamao River, Mt. Mariveles, Borden FB 2562 (BO, K, SING, ♀), 2915 (NY, US, ♂), 2498 (BO, K, P, SING, ♂). Pampanga: Camp Stotsenburg, Mt. Pinatubo, Elmer 22030 (BM, GH, L, ♂, ♀). Rizal: Ahern FB 3197 (BO, K, SING, US, ♀); Morong district, Vidal 3832 (K, US, ♀); San Mateo, Vidal 1548 (A, K, L, ♂). Batangas: Ramos & Deroy BS 22656 (A, BM, GH, K, L, P, SING, ♂). Camarines: Alvarez FB 21440 (BM, BO, K, P, ♂, ♀), Ramos 1517 (BM, BO, GH, L, P, SING, ♂, ♀). Albay: Banao, Guinabatan, Mendoza PNH 18505 (L, PNH, ♀). Sorsogon: Curran FB 10524 (K, SING, ♀), Vidal 3839 (K, ♂); Irosin, Vidal 3836 (K, ♀); Irosin, Mt. Bulusan, Elmer 15598 (A, BM, K, L, ♂, ♀), Sulit PNH 2753 (A, BO, PNH, SING, ♀).

Although, as was pointed out in the discussion of section *Pseudojaca*, *Artocarpus rubrovenius* shows a relationship with *A. lakoocha*, it is readily distinguished by the glabrous leaves lacking a prominent reticulum, and, at anthesis, by the shorter styles. The differences from the other glabrous-leaved members of subgenus *Pseudojaca* that occur in the Philippines, *A. xanthocarpus* and *A. nitidus* ssp. *nitidus*, are given under the latter entity.

Merrill stated in 1923 that *Artocarpus rubrovenius* occurred on Mindoro and Cagayan Sulu, in addition to Luzon. The former record may be based on the two collections cited by Merrill that have not been seen, Darling FB 14704 and Merrill 1517. It is presumed, from the identification on the herbarium sheet, that the latter is based on Merrill 5304, although the number was not cited. This collection is here referred to *A. gomezianus* ssp. *gomezianus*.

40. *Artocarpus fulvicortex* Jarrett, sp. nov.

Artocarpus sp., Corner, Wayside Trees, 658, t. 197. 1940.

Ramuli juniores puberulentes; folia late elliptica vel subrotunda, nervis lateralibus utrinque 6–10, nervis transversalibus paucis, costa nervis lateralibus venulisque subtus valde prominentibus, pubescentibus, intervenio saepe minute pubescenti; inflorescentiae subsessiles; capitula mascula subglobosa, 4–6 mm. diametro; syncarpia globosa, superficie plana, pubescentia, bracteis persistentibus.

Arbores [ad 35 m. altae], deciduae, cortice nova fulva vel rufi-brunnea. *Ramuli juniores* 4–8 mm. crassi, subrugosi, puberulentes, cortice in sicco mox squamis decidua; [ramuli juveniles pubescentes]. *Folia* c. 15 × 10 [10–20 × 7–14] cm., late elliptica vel subrotunda, obtusa vel breviter acuminata, basi cuneata [vel rotunda], integra, supra subglabra, costa nervis lateralibusque pubescentibus exceptis, subtus costa nervis lateralibus venulisque valde prominentibus, pubescentibus, pilis rufis, interdum sparsis, intervenio minute pubescenti vel puberulenti, [foliis juvenilibus subglabro], supra saturata viridia, subtus subglaucula, in sicco utrinque rufi-brunnea vel caesia; nervi laterales utrinque 7 [6–10], curvati; nervi transversales pauci, paralleli vel reticulati; petiolus 20 [15–25] mm. longus.

Inflorescentiae axillis foliorum solitariae vel geminae. *Ad anthesin: capitula mascula* 4–7 × 4–6 mm., globosa vel obovoidea; perianthia profunde bifida, 0.7 mm. longa, breviter ciliata; stamina 0.8 mm. longa, filamentis supra attenuatis, cellis antherum ellipsoideis, 0.15 mm. longis; bractee crasse stipitatae, capitibus peltatis, ad 0.5 mm. latis, breviter ciliatis; pedunculus 0.5–1.5 × 1 mm., breviter pubescens; *capitula feminea* stylis inter bracteas peltatas crebras 0.5 mm. exsertis. [*Syncarpia* ad 5 cm. diametro, globosa, fulva, carne lutea, in sicco rufi-brunnea, superficie plana, pubescenti, bracteis numerosis persistentibus, inconspicuis, in indumento immersis; stratum externum syncarpium c. 5 mm. crassum; "semina" (endocarpia cornea) plura, obovoidea, 10 × 5 mm., perianthiis omnino conjunctis inclusa; axis syncarpium c. 15 mm. diametro; pedunculus 4 × 4 mm., breviter pubescens.] (*Inflorescentiae* typi anthesin atque syncarpium maturum (Corner SFN 34663) ab eadem arbore collectum omnes spiritu vini conservae descriptae.)

HOLOTYPE: Malaya, Corner SFN 33686 (SING).

DISTRIBUTION: in lowland evergreen forest to 250 ft.; Malaya, Sumatra, Banka.

Malaya. PERAK. Batu Gajah, Corner, Aug. 1936 (SING); Slim River, Corner, Aug. 1937 (SING). PAHANG. Kemansul For. Res., Symington KEP 49822 (KEP). NEGRI SEMBILAN. Seremban, Walton KEP 63363 (KEP, ♀). MALACCA. Main-gay 1485 (K). SINGAPORE. Cantley (SING); Cluny Road, Ridley 4829 (BM, CAL, SING, ♀); Chanchu Kang, Ridley 4129 (K, SING, ♂, ♀); Krangi, Goodenough 3379 (CAL, SING); ne. end of MacRitchie Reservoir, Sinclair SFN 38916 (SING, L, ♂); Reservoir Jungle, Corner, Jan. 1937 (SING). Sumatra. PALEMBANG. Ban-

juasin, Bentajan, *NIFS T 1030* (BO); Lematang Ilir, Gunong Megang, *NIFS T 364* (BO, L, ♂), *592* (BO, L, U, ♂, ♀). LAMPONGS. Kotabumi, *bb 35005* (BO); Tulang Bawang Ilir, Bandjar Agung, *bb 8951* (BO). BANKA. Blinju, *Grashoff 20* (BO, L); Koba, *Teysmann HB 7242* (BO, C, CAL, K, L); Muntok, Batu Balai, *Teysmann HB 6843* (BO, CAL, K, L, P). **Cultivated.** MALAYA. Singapore, Hort. Bot. (all from tree in potting yard), *Corner SFN 33686*, Sept. 1937 (SING, ♂, ♀), *34501, 34663* (SING, ♀), *Merah SFN 33549* (SING).

This species was described as *Artocarpus* sp., "Orange-barked *Tampang*," in 1940 by Corner, who stated (p. 650) that the bark colour was distinctive, since it was grey or brown in other Malayan species of the genus. The broadly elliptic or subrotund leaves, with few lateral veins and a markedly prominent reticulum on the lower surface, have a characteristic appearance which enables this species to be identified readily when sterile. However, no previous description under a scientific name has been found, and specimens have been identified as either *A. lakoocha* or *A. dadah*. *Artocarpus fulvicortex* differs from the latter in the leaf characters given above, and also in the very short peduncles of the inflorescences, the numerous bracts persisting on the syncarp and the nearly glabrous young twigs.

41. *Artocarpus tomentosulus* Jarrett, sp. nov.

Differt ab *A. fulvicortice* foliis ellipticis, elliptici- vel ovati-oblongis, nervis lateralibus utrinque 10–14, nervis transversalibus plurimis, syncarpio pedunculo 25 mm. longo.

Arbores ad 20 m. altae. *Ramuli juniores* 2.5–4.5 mm. crassi, rugosi, puberulentes. *Folia* c. 18×10 [$11\text{--}23 \times 6\text{--}12$] cm. elliptica ad elliptici- vel ovati-oblonga, acuminata [acumine ad 2 cm. longo], basi rotunda [vel late cuneata], integra, supra glabra, costa nervis lateralibusque pubescentibus exceptis, subtus costa nervis lateralibus venulisque prominentibus, pubescentibus, intervenio minute tomentoso [vel glabro], in sicco supra pallidi- vel rufi-brunnea, subtus pallidi-brunnea; nervi laterales utrinque c. 12 [10–14], curvati; nervi transversales plurimi, paralleli; petiolus 15[–45] mm. longus.

Inflorescentiae axillis foliorum solitariae. [*Capitula mascula* (immatura) ad 7 mm. diametro, globosa; perianthia tubulosa, 0.6 mm. longa, supra bilobata, minute pubescentia; stamina (nondum exserta) cellis antherum ellipsoideis, 0.15 mm. longis; bractae tenuiter stipitatae, capitibus peltatis, ad 0.4 mm. latis, minute pubescentibus; pedunculus c. 2×2 mm., brevissime pubescens.] *Syncarpium* (submaturum) 3 cm. diametro, subglobosum, fulvum, in sicco brunneum, superficie parum papillosa, pubescenti, bracteis peltatis plurimis persistentibus; pedunculus 25×3.5 mm., breviter pubescens.

HOLOTYPE: British North Borneo, *Keith 7671* (SING).

DISTRIBUTION: in forest to 2000 ft.; endemic to northeastern Borneo.

Borneo. EAST AND NORTHEAST BORNEO. Berouw: *bb 18909* (A); Bekmuari, *bb 19133* (A, BO, L). Bulungan: Mara, *bb 10806* (BO). BRITISH NORTH BORNEO. Kabili-Sepilok For. Res., *Keith 7671*, Sept. 1937 (SING, ♀); Kalabakan, 30 miles wnw. of Tawau, *Wood SAN A 3684* (A, KEP, L, SING, ♂).

The material of *Artocarpus tomentosulus* is very limited, but the collections are well characterized by the leaves, which have fairly closely set, spreading lateral veins with numerous parallel, rather slender intercostals. The type, *Keith 7671*, bears a submature syncarp, and this specimen and *bb 10806*, which is sterile, have the intervenium minutely tomentose. The remaining collections, *Wood SAN A 3684* (with male inflorescences), *bb 18909* and *bb 19133* (sterile), have a glabrous intervenium. It is possible that the latter are taken from juvenile shoots, since the leaves are somewhat larger than in the previous collections. If these three collections are matched with the other two on the basis of the venation, as seems justifiable, the characters of this species correspond with those of *A. fulvixortex* in the small, subsessile, more or less globose male heads, and in the combination of prominent, patent-pubescent venation on the lower surface of the leaf with a frequently minutely tomentose intervenium, although the syncarp peduncle is considerably longer (25 mm. instead of 4 mm.). These leaf characters are unique in the subgenus; in other species with a tomentose intervenium (*A. glaucus*, *A. hypargyreus* and *A. styracifolius*) the venation is less prominent, and the main veins, at least, are subglabrous. Collections of *A. dadah* from Borneo (which can be distinguished by the narrower leaves and the pubescent twigs) may also appear to have hairs on the intervenium of the leaf, but these are nearly all inserted along the edge of the veins of the reticulum and appressed over the areolae.

42. *Artocarpus glaucus* Blume, Bijdr. 483. 1825, "*glauc*"; Tréc. Ann. Sci. Nat. Bot. III. 8: 121. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 90, 96. 1854; Miq. Pl. Jungh. 293. 1854, Fl. Ind. Bat. 1(2): 288. 1859, Ann. Mus. Lugd.-Bat. 3: 212. 1867; Koord. & Val. Bijdr. Boomsoort. Java 11: 26. 1906; Backer, Beknopte Fl. Java 6: 16. 1948. Neotype, Java, *Zollinger 704* (P).

Artocarpus glaucescens Tréc. Ann. Sci. Nat. Bot. III. 8: 120. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 90. 1854; Miq. Fl. Ind. Bat. 1(2): 288. 1859, Ann. Mus. Lugd.-Bat. 3: 212. 1867; Renner, Bot. Jahrb. 39: 369. 1907. Holotype, Java, *Zollinger 704* (P); isotypes (BM, GH, K, L, P).

Artocarpus zollingeriana Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 90, 95, 1854; Miq. Fl. Ind. Bat. 1(2): 289. 1859. Syntypes, Java, *Zollinger 512* (P), Bogor, Hort. Bot., *Zollinger s.n.* (V); lectotype, *Zollinger 512* (P).

Artocarpus biformis Miq. Fl. Ind. Bat. Suppl. 419. 1861. Holotype, Sumatra, *Teysmann HB 4444* (V); isotypes (BO, L).

Artocarpus tephrophylla Miq. Fl. Ind. Bat. Suppl. 422. 1861. Holotype, Sumatra, *Teysmann 4504* (V); isotypes (BO, L).

Artocarpus inaequalis Teysm. & Binnend. Cat. Hort. Bog. 382. 1866, nomen nudum.

Artocarpus glaucescens Tréc. var. *tephrophylla* Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867.

Artocarpus denisoniana King in Hook. f. Fl. Brit. Ind. 5: 544. 1888; King, Ann. Bot. Gard. Calcutta 2: 14. t. 8B. 1889; Ridley, Fl. Malay Penin. 3: 355. 1924. Syntypes, Malaya, *King 10318, 10843, 10987* (CAL, not seen; duplicates examined, K, etc.).

Artocarpus glaucus Blume var. *villosiusculus* Warb. ex Renner, Bot. Jahrb. 39: 369. 1907, nomen nudum.

Evergreen trees, height to 40 m., buttressed or not, bark dark grey, peeling. *Twigs* 1.5–4 mm. thick, finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 4–33 × 2–16 cm., elliptic to elliptic-oblong, varying to oblong, obovate, ovate, or ovate-lanceolate, small leaves often rather narrow, acuminate or attenuate, base cuneate, varying to rounded, often slightly unequal and decurrent, margin entire; juvenile leaves lobed; main veins prominent beneath, intercostals slightly so; glabrous above, venation appressed-puberulent beneath, glabrescent, intervenium minutely tomentose (juvenile leaves subglabrous to short-pubescent beneath); lateral veins 8–15 pairs, curved; intercostals parallel; old leaves becoming bullate above between venation; glossy dark green above, light green to dull grey beneath, drying yellowish to bluish grey above, greyish glaucous beneath from the tomentum, young leaves brown with nigrescent main veins; petiole 7–25 (–45) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 11–24 × 5–6 mm., narrowly oblong or clavate; perianths 2- or 3-lobed, divided nearly to the base, 0.6 mm. long; stamen 0.8 mm. long, filament cylindric, contracted above, anther-cells ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, these and perianths short-ciliate; peduncle 1–3 × 1 mm., velutinous; *female head* with styles exerted to 0.3 mm. through a dense covering of peltate bracts, later through papillae emerging between bracts. *Syncarp* to 3 cm. (fide Koorders & Valetton, 1906, to 7 cm.) across, subglobose, often shallowly lobed, yellow to orange-brown with light-orange flesh, drying dark brown to black, the surface papillate or becoming nearly smooth, short-pubescent, with numerous persistent bracts; wall c. 3 mm. thick; proximal region of perianths free, fruiting perianths several, "seeds" (horny pericarps) ellipsoid, 10 × 7 mm.; core c. 10 mm. across; peduncle 2–5 × 2 mm., velutinous.

VERNACULAR NAME: *tiwu landu* (Sundanese), Java.

DISTRIBUTION: in evergreen forest to 2500 ft., Malaya, Sumatra, Simalur, Banka, Borneo, Java, Lesser Sunda Islands (Sumba, Roma, Tanimbar Islands).

Malaya. KEDAH. Katumbah, *Meh 17874* (K, SING, ♂). PERAK. Ulu Bubong, *King 10161* (A, SING, ♀), *10318*, June 1886 (BM, K, L, ♂, ♀), *10843*, Aug. 1886 (BM, K, ♀), *10987*, 1886 (K, P, SING, ♂, ♀). PAHANG. Bentong, *Ahmad CF 5052* (K, ♂); 3 miles s. of Kuala Lipis, *Burkill & Haniff SFN 17168* (BO, K, SING, ♂, ♀). SELANGOR. Ulu Gombak, *Murdoch 304* (SING, ♂, ♀). JOHORE.

10½ miles Kota Tinggi-Jemalaung road, *Sinclair SFN 40348* (K, L, SING, ♂, ♀).

Sumatra. TAPANULI. Padang Lawas, Hatiran, *Rahmat si Boeea 4883* (A, K, L, ♀), *4920* (A, K, L, ♂). WEST COAST. Priaman, *Diepenhorst HB 1325* (BO, L, P, U). EAST COAST. Aer Kandis, near Rantau Parapat, Bila, *Rahmat si Boeea 2467* (A, L, SING, ♂, ♀); Sibolangit, *Docters van Leeuwen-Reijnvaan 12711* (BO, K, L, ♂), *Lörzing 5170* (BO, ♂). DJAMBI. Danau Lama, *bb 13643* (BO); Simpang, *bb 13115* (BO). BENKULEN. Kroï, Gunong Nemala, *bb 8758* (BO); Ranaumeer, Talangtotong, between Simpang and Sepatuhu, *Van Steenis 3378* (BO, ♀). PALEMBANG. Lematang Ilir, Gunong Megang, *NIFS T 886, 891* (BO, L, ♀); Musi Ilir, Muara Punojung, *bb 9202* (BO); Musi Ulu, *Endert 159* (BO). LAMPONGS. Kalianda, Gunong Kadjabasu, *De Wit 14* (BO); Kalianda, Ketjapi, *bb 8954* (BO, L); Siring Kebou, *Teysmann HB 4504* (BO, L, U); Tarabangi Ilir, *Teysmann HB 4444* (BO, L, U). SIMALUR. Achmad *966* (BO, K, L, SING, U, ♂, ♀); Landschap Tapah, Defajan, *Achmad 1405* (BO, L, U, ♂, ♀), *1675* (BO, L, P, ♂), *1721* (BO, L, SING, ♂, ♀). BANKA. S. Banka, Rindik, *bb 11585* (BO).

Borneo. SARAWAK. Sungei Sama, *Daud & Tachun SFN 35729* (SING, ♀). WEST BORNEO. Ketapang, Riamdadap, *bb 8306* (BO); Sambas, Sai, *bb 7086* (BO, L, ♂). SOUTH AND SOUTHEAST BORNEO. Bandjarmasin, *Motley 1279* (CGE, K, ♂, ♀); Muara Tewe, Dusun Ulu, Sungei Pararawen, *Dachlan 2411* (L). BRITISH NORTH BORNEO. *Wood 2159* (BO, ♂, ♀); Beaufort south mile 18, *Wood 2608* (SING, ♂); Tenom, Pangie, *Angian Herb. For. Dept. B.N.B. 10482* (KEP, ♂).

Java. *Hasskarl HB 1869* (L), *De Vriese* (K, L, U), *Zippelius 1332* (HB 7267) (BO), *Zollinger 512* (P, ♂), *701* (K), *s.n.* (K, L, P, U). WEST JAVA. Bantam: Gunong Kantjana, *Koorders 41644* (BO); Gunong Mung, Gunong Karang, Pulasari, *Koorders 40118* (BO, L); Tapos, *Teysmann HB 7268* (BO); Tjibadui, Kosala, *Forbes 450* (BM, BO, CAL, SING, ♂, ♀); Tjikoja, *Zollinger 704* (BM, GH, K, L, P, ♂), *706* (U); Tjimara-Udjong Kulon, Gunong Marang, *Koorders 8672* (BO, L, P); Tjimara-Udjong Kulon, Gunong Rompong, *Koorders 8671* (A, BO, L, P) *9932* (BO). Buitenzorg: Leeuwiliang, Pasir Honje, *Bakh. van den Brink 6953* (BO, K, L, P, SING, U, ♂); Nangala, *Bakh. van den Brink 7629* (BO, L, ♀); Nangala, Gunong Menteng, *Bakh. van den Brink 7717* (BO, K, L); Nangala, Gunong Tjiputih, *Bakh. van den Brink 7726* (BO, K, L, P, U, ♂, ♀); Nangala, Tjilankop near Tjiputih, *Bakh. van den Brink 7719* (BO); Tjibinong, *NIFS Ja 2702* (BO, ♀). Preanger: Sukabumi, Tjisahong, Tjisalak, *Koorders 39445* (BO, K, L, P, ♀); Njalidung, *Uhl 6555* (BO, ♀). CENTRAL JAVA. Banjumas: Bandjarnegara, Pagedongan, *NIFS Ja 2549* (A, BO); Bandjarnegara, Pringombo, *Koorders 8673* (BO, L), *33881* (BO), *39184* (BO, K, L), *39194* (BO, L, P). Pekalongan: Subah, Pesan, *Koorders 27594* (BO, L, P, ♀). Semarang: Ungaran, Telomojo, *Koorders 39234* (A, BO, K). EAST JAVA. Pasuran: Tangkil Zuidergebergte, *Koorders 23784* (BO).

Lesser Sunda Islands. SUMBA. E. Sumba, Djuli, *bb 15133* (BO). ROMA. Hila, *bb 7219* (BO). TANIMBAR ISLANDS. P. Jamdena, between Kampong Ilgnei and Otimmer, *Buwalda 4131* (K, L, ♂, ♀) = *bb 24224* (A, BO, L, SING, ♀). **Cultivated.** JAVA. Bogor, Hort. Bot., *Teysmann HB 7274* (BO, P, ♀), *s.n.*, 1867 (BM, L, ♀), *Zollinger* (U).

No collections determined as *Artocarpus glaucus* by Blume himself have been found, but the description is clearly identifiable. The glaucous lower surface of the leaf distinguishes this species from any other member of the genus growing in Java, and, with the elongate, subsessile male head,

from the rest of subgenus *Pseudojaca*. The leaves vary considerably, but continuously, in shape from tree to tree, and they also become markedly coriaceous with age. Several specimens bear what appear to be galled shoots. These are short and highly branched, and bear many inflorescences, which are usually male, but are abnormally shaped. The heads are obovoid with peduncles to 5 mm. in length, and the flowers are often malformed.

43. *Artocarpus nitidus* Tréc. Ann. Sci. Nat. Bot. III. 8: 119. 1847.

Evergreen trees, height to 35 m., buttressed or not, bark red-brown. *Twigs* 1–4 mm. thick, smooth or finely rugose, appressed-puberulent, soon glabrescent. *Leaves* 3.5–23 \times 1.5–9 cm., elliptic, obovate- or oblong-elliptic, to obovate- or ovate-oblong, obtuse to attenuate or with an acumen to 2.5 cm. long, base cuneate or rounded, margin entire; main veins prominent beneath, intercostals slightly so; glabrous, or puberulent beneath on the main veins (rarely throughout in ssp. *lingnanensis*); lateral veins 5–15 pairs, straight or curved; intercostals few, usually parallel; dark green above, paler or yellowish green beneath; petiole 5–15 (–25) mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* 3.5–12 \times 2.5–7 mm., oblong, obovoid or clavate; perianths of 2–4 segments free or fused at the base, 0.5–0.7 mm. long; stamen 0.8–1 mm. long, filament broad, tapering or contracted above, anther-cells short-ellipsoid, 0.2 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, these and perianths ciliate; peduncle 1–3 \times 1 mm.; *female head* with the styles exerted to 0.5 mm. through a covering of peltate bracts, or through perforations or low papillae, the bracts scattered. *Syncarp* 1.5–6 cm. across, subglobose, the surface smooth, with scattered persistent bracts, the indumentum various; wall 1–5 mm. thick; proximal region of perianths free, fruiting perianths 1–12, thin-walled, “seeds” (pericarps with a horny endocarp), subglobose to ovoid, 8–10 \times 7–8 mm.; core 5–8 mm. across; peduncle 1.5–4 (–20) \times 1.5–3 mm.

DISTRIBUTION: in forest or savannah to 5000 ft.; Assam, Burma, Siam, Indochina, southern China, Malaya, Sumatra, Borneo, northern and central Philippines.

Four taxa which have previously been recognized as species (with several additional synonyms) are here reduced to subspecific rank under *Artocarpus nitidus*, since they are only separable from this species and from each other on the size and indumentum of the syncarp, and on slight differences in the shape and venation of the leaves. The type subspecies, which occurs in the Philippines, is readily distinguished by the very small, few-seeded, velutinous syncarp. The two subspecies placed following this, ssp. *lingnanensis*, which extends from southern China to peninsular Siam, and ssp. *humilis*, which is restricted to Borneo, appear to be very closely allied to each other. They have larger, also velutinous

syncarps, and are distinguished only by minor, but characteristic, differences in the leaves. However, in view of the variation found in the length of the female peduncle in ssp. *humilis* (discussed under the subspecies), it seems best to retain them as distinct taxa of equal rank for the present. The remaining subspecies, which usually have more numerous lateral veins in the leaves than the three preceding entities, are ssp. *borneensis*, from Borneo, and ssp. *griffithii*, extending from Yunnan and Indochina to Sumatra and Borneo. They are likewise very closely related, differing only in the indumentum of the syncarp. In ssp. *borneensis* the surface is densely covered by minute hairs with readily deciduous, multicellular, clavate heads which, when fallen, often form a reddish powder around the dried syncarp. These hairs are presumably equivalent to the gland-hairs occurring generally within *Artocarpus*, although in subg. *Pseudojaca* the heads of the latter are usually unicellular. In ssp. *griffithii*, on the other hand, the syncarp is almost entirely glabrous.

The occurrence of three subspecies in Borneo has led to difficulties in identification which are increased by the finding of specimens, all bearing very small, elliptic, long-acuminate leaves, which are referable on the characters of the syncarp to all three entities. Larger-leaved collections of ssp. *humilis*, lacking or bearing only male inflorescences, can be distinguished on vegetative characters, but no such characters have been found that would separate ssp. *borneensis* and ssp. *griffithii*. Collections from Borneo which lack syncarps and which are referable to one or other of these subspecies, are listed separately under ssp. *borneensis*. There are, in addition, a few male or sterile collections from Borneo and elsewhere that could not be identified to subspecies and have not been cited. On the evidence of specimens bearing syncarps (none seen from western Borneo), ssp. *borneensis* is relatively common in British North Borneo, whereas ssp. *griffithii* is absent there, though widely distributed outside Borneo. The provenance of the small-leaved collections appears to be variable, since Corner noted for ssp. *griffithii* (Wayside Trees, 654. 1940, as *A. gomezianus*) that such specimens came from the crowns of large trees, whereas Beccari derived the specific epithet for *A. humilis*, of which the type has small leaves, from its being a small tree.

Three collections referable to *Artocarpus nitidus* have been seen from Burma and Assam, but they bear only male inflorescences and, from the shape of the leaves, might represent either ssp. *lingnanensis* or ssp. *griffithii*. They are: *Dickason* 6938, 6981, Rangoon (A, ♂); *Kanjilal* 1145, Makum Range, Barjan, Lakhimpur (κ, ♂). A collection from the Lushai Hills, *Sen Gupta* 7643, is cited by *Kanjilal et al.*, Fl. Assam 4: 269. 1940, as *A. gomeziana* Wall. var. *griffithii* King (= ssp. *griffithii*).

KEY TO THE SUBSPECIES OF *ARTOCARPUS NITIDUS*

1. Syncarp to 1.5(-3) cm. across, velutinous, seeds 1-3(-6). ssp. *nitidus*.
1. Syncarp larger, seeds more numerous.
 2. Syncarp velutinous; larger leaves with 5-11 pairs lateral veins.

3. Leaves obtuse to shortly and bluntly acuminate. . . ssp. *lingnanensis*.
3. Leaves with an acumen to 2.5 cm. long, lateral veins often markedly ascending ssp. *humilis*.
2. Syncarp not velutinous; larger leaves with 8-15 pairs lateral veins.
4. Syncarp covered by readily deciduous, clavate hairs. . . ssp. *borneensis*.
4. Syncarp subglabrous. ssp. *griffithii*.

ssp. *nitidus*

Artocarpus nitidus Tréc. Ann. Sci. Nat. Bot. III. 8: 119. 1847, "*nitida*"; Miq. Fl. Ind. Bat. 1(2): 288. 1859; Fern.-Villar, Noviss. App. 203. 1880; Vidal, Revis. Pl. Vasc. Filip. 254. 1886; Renner, Bot. Jahrb. 39: 368. 1907; Elmer, Leaf. Philip. Bot. 2: 624. 1909. Syntypes, Luzon, *Cuming 1078*, 1081 (p); lectotype, *Cuming 1078* (p).

Artocarpus lanceolata Tréc. Ann. Sci. Nat. Bot. III. 8: 121. 1847; Miq. Fl. Ind. Bat. 1(2): 288. 1859; Fern.-Villar, Noviss. App. 203. 1880; Vidal, Revis. Vasc. Pl. Filip. 255. 1886; Elmer, Leaf. Philip. Bot. 2: 624. 1909. Holotype, Luzon, *Callery 60* (p); isotype (p).

Artocarpus lamellosa auct. non Blanco, Merr. Publ. Gov. Lab. Manila 27: 80. 1905, Sp. Blancoanae, 124. 1918, Enum. Philip. Pl. 2: 41. 1923.

Leaves 4-13 \times 2-5.5 cm., obovate-oblong, with an acumen to 1.5 cm. long, base rounded, varying broadly cuneate, margin entire; juvenile leaves to 16 \times 7.5 cm., denticulate towards the apex; lateral veins 6-9 pairs, curved; drying brown to blue-grey above, brownish or greenish below, the venation often straw-coloured, reddish in some young leaves. *Male head* 6-10 \times 3 mm., oblong or clavate; peduncle 1-2 \times 1 mm., velutinous. *Syncarp* to 1.5(-3) cm. across, drying light brown or cinereous, short-pubescent; seeds 1-3(-6); peduncle 2(-6) \times 1.5 mm., velutinous.

DISTRIBUTION: in forest to 500 ft.; northern and central Philippine Islands.

Philippine Islands. LUZON. Ilocos Norte: Burgos, *Ramos BS 27283* (A, BO, P, ♂). Abra: *Valera PNH 13846* (A, PNH, ♀). Pangasinan: *Lopez FB 24217* (A, ♂, ♀), *Medina FB 13503* (US, ♂). Rizal: Calawan, *Callery 60*, 1840 (P, ♂). Cavite: Maragondong, *Merrill 4167* (BM, L, P, US, ♂). Batangas: *Merrill SB 100* (A, BM, BO, GH, K, L, P, ♂, ♀); Lobo, *Vidal 1540* (A, K, L, ♂, ♀). Laguna: Mt. Makiling, *Canicosa PNH 9802* (A, PNH, ♂), *Elmer 18279* (A, BM, K, L, ♂, ♀), *Sulit PNH 16923* (PNH). Albay: *Cuming 1078* (BM, CGE, K, L, P, SING, ♂), 1081 (BM, CGE, K, L, P, SING, ♂, ♀). TABLAS. *Cortes & Rendal FB 17845* (K, US, ♂, ♀). CEBU. *Lopez & Reyes FB 27333* (SING), *Ramos BS 11022* (BM, K, ♂). PANAY. Miagao, Ilo-ilo, *Vidal 3834* (A, K, ♂, ♀). GUIMARAS. *Sulit PNH 11697* (A, L, PNH, ♂, ♀); Buenavista, Bo. Salvacion, So. Lande, *Sulit PNH 11832* (A, L, ♂, ♀).

Artocarpus nitidus was reduced by Merrill in 1905 to the earlier *A. lamellosa* Blanco which has, since then, been accepted as the correct name for the species (in the restricted sense of *ssp. nitidus*). In making this identification Merrill was following Fernandez-Villar, who in 1880 had also regarded the two species as synonymous, although he retained Trécul's name. However, while Blanco's description undoubtedly refers to one of the three glabrous-leaved members of subg. *Pseudojaca* that occur in

the Philippines, it does not agree with the entity under consideration. *Artocarpus lamellosa* was described as having a fruit the size of a hen's egg, which was full of seeds, whereas in *A. nitidus* ssp. *nitidus* the syncarp does not usually exceed 1.5 cm. in diameter or have more than three seeds. The account could apply to either of the two other species, *A. xanthocarpus* Merr. (1904) or *A. rubrovenius* Warb. (1905), but no characters are given that would differentiate between them. In view of the long-standing misidentification it seems best, therefore, to reject *A. lamellosa* as a *nomen dubium*.

Artocarpus nitidus ssp. *nitidus* has frequently been confused with *A. xanthocarpus*, but the latter is distinguished by the globose to obovoid, rather than oblong or clavate male head ($3-6 \times 3-4$ mm. vs. $6-10 \times 3$ mm.), by the longer styles (exserted to 0.8-1 mm. vs. 0.5 mm.), and by the larger syncarp (to 5 cm. vs. 1.5(-3) cm. across) with a longer peduncle (6-11 mm. vs. 2(-6) mm.) and several (instead of 1-3(-6)) seeds. In *Artocarpus nitidus* ssp. *nitidus* the leaves are usually obovate-oblong with a rounded base, and dry (when mature) blue-grey above and light brown beneath; in *A. xanthocarpus* the leaves are longer and narrower in outline, with a cuneate or sometimes narrowly rounded base, and they dry brown or greenish on both surfaces. Merrill, in 1923, reduced *A. xanthocarpus* to *A. lanceolata* Tréc. but examination of Trécul's type has shown that it is merely a collection of *A. nitidus* ssp. *nitidus* with rather narrow leaves, the male inflorescences being characteristic of the latter entity. *Artocarpus rubrovenius* can be distinguished from both these taxa by the larger male inflorescences and leaves, the latter often having a broadly rounded and oblique base.

The specimen *Borden FB 2946* (BO, SING), which Merrill cited in his enumeration of the flora of the Lamao Forest Reserve (Philip. Jour. Sci. 1, Suppl. 43. 1906) under *A. lanceolata* (as a species distinct from *A. nitidus* and *A. xanthocarpus*) must be referred to *Antiaris toxicaria* Lesch. Elmer (1909) cited under *A. lanceolata*, with some doubt, *Borden 1145* from the same locality, but, unless this is the field number of the same collection, no specimens have been seen in the course of this study.

ssp. *lingnanensis* (Merr.) Jarrett, stat. nov.

Artocarpus parva Gagnep. Bull. Soc. Bot. Fr. 73: 89. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 735. fig. 90. 1928. Syntypes, Tonkin (cultivated), *Balansa 740, 4112, 4544, Bon 412, 466, Fleury 37765* (p); lectotype, *Balansa 4112* (p).

Artocarpus sampor Gagnep. Bull. Soc. Bot. Fr. 73: 90. 1926, excl. syncarp.; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 738. 1928. Syntypes, Cambodia, *Chevalier 31915, 36953, Fleury 30049, Cochinchina, Pierre 1637* (excl. syncarp), Annam, *Poilane 6879*, Siam (cultivated), *Thorel 2784* (p); lectotype, *Poilane 6879* (p).

Artocarpus lingnanensis Merr. Lingnan Sci. Jour. 7: 302. 1931, 13: 56. 1934. Syntypes, Kwangtung (cultivated), *McClure 13471* (uc, not seen; duplicates examined, K, P), Honam Island, *McClure s.n.*, Sept. 1924 (uc, not seen).

Leaves 6–14 \times 3.5–8 cm., elliptic to oblong- or obovate-elliptic, the outline often somewhat irregular, obtuse or shortly and obtusely acuminate, base rounded or cuneate, usually slightly decurrent, margin entire or shallowly and irregularly crenate; lateral veins 6–10 pairs, straight or curved; drying brown or grey, venation concolorous or, in young leaves, nigrescent. *Male head* 4–12 \times 3–4 mm., obovoid, varying oblong; peduncle 1–1.5 \times 1 mm., velutinous. *Syncarp* to 5 cm. across, red with pink flesh, drying brown, velutinous; seeds c. 5–12; peduncle 1.5–3 \times 2 mm., velutinous.

VERNACULAR NAMES: *ma hat*, Siam; *sampor*, Cambodia; *cay chay*, Annam; *hung kwai muk*, *kwai muk*, southern China. USES: planted for the edible fruit; the bark and roots are also added to betel.

DISTRIBUTION: in evergreen and mixed forest, and in savannah, to 3000 ft.; Siam, Indochina, southern China (Kwangtung, Hainan); cultivated, especially in Tonkin.

Siam. Chantaburi, Klung, *Kerr* 17956 (BM, ♀); Chantaburi, Ma Kaun Kaim, *Kerr* 493 (BM, ♂); Kao Ngon, Loi, *Kerr* 8795 (BM, ♂); Ko Chang, *Schmidt* 129 (c); Sriracha, *Collins* 892 (US, ♀). PENINSULAR SIAM. Krabi, Tambon Kao Panom, *Kerr* 18647 (BM, ♀); Satul, Kuan Po, *Kerr* 13809 (BM, ♂); Surat, Tha Chang, *Ratn* 2373 (CGE, ♂). INDOCHINA. CAMBODIA. *Béjeaud* (p, ♀). Kompong Chnang Prov.: near Kompong Chnang, *Chevalier* 31915, Mar. 1914 (p, ♀); Kralanh For. Res., *Fleury* 30049, Mar. 1914 (p, ♀); Prey Chang Ka Tamau, *Chevalier* 36953, Jan. 1918 (p, ♂, ♀); Prey Phum Laung, *Chevalier* 36903 (p, ♂). Stung Treng Prov.: between Pra Pranap and Chéom Khsan, *Poilane* 14881 (p, ♂). COCHINCHINA. Bien Hoa Prov.: Song Lu, *Pierre* 1637, Mar. 1877 (K, p, US, all with fruit of *A. gomezianus* ssp. *gomezianus* [A, sterile twig of *A. gomezianus*]). ANNAM. Kontum Prov.: between Zakha and Dakto, *Poilane* 32307 (p, ♂). Nhatrang Prov.: peninsula of Nui Han Heo, *Poilane* 6879, June 1923 (A, p, ♀); near Pham Rang, *d'Alleizette*, June 1919 (p, ♀). TONKIN. Phu Tho Prov.: Trung-Giap For. Res., *Fleury* 37615 (p, ♀).

China. KWANGTUNG. Near Canton, *Levine* 2807 (A, ♂), 2124 (A, GH, K, ♀); Chung Shan Ooi T'ung, *Fung Hom* 68 (NY, ♀); Heungshan, *Chun* 1 (NY); Honam Island, *Levine* 1009 (A, GH, US, abnormal infl.). HAINAN. *Wang* 32813 (A, NY, p, ♀); Ch'ang-kiang district, Ue Lung Ling, *Lau* 1349 (A, BM, p, ♂); Kan-en district, Chim Fung Ling, *Lau* 3385 (A, p, ♂), 5644 (A, ♀); Kaingchow, *Henry* 8255 (K, p, ♀); Lokwui, *How* 72283 (A, ♀); Man Ch'ung district, *McClure* 20016 (K, ♂); near Manning, *How* 71529 (A, SING, ♂); Ngai district, Ko Leng, *Lau* 566 (A, BM, K, p, US, ♀); Yiachow, *Liang* 62103 (A, NY, p, US, ♀).

Cultivated. SIAM. Ubon, Kemmarat, *Thorel* 2784, 1866–1868 (A, p, ♂). INDOCHINA. Cochinchina: Saigon, Hort. Bot., *Pierre* 18 (p), *Ciep* 553 (p, ♀). Annam: Haut Douai Prov., Laonan, *Poilane* 23405 (p, ♂), near Tourane, *Clemens* 3369, 3988 (A, ♀). Tonkin: Hanoi and vicinity, *d'Alleizette*, May 1908 (L), *Balansa* 740, July 1885 (p, abnormal infl.), 4112, May 1889 (p, ♂), 4544 (p, ♀), *Fleury* 37765, Apr. 1918 (p, ♂); Ninh-binh Prov., Ton Duc, *Bon* 412 (p, ♂), Ninh-binh Prov., Yen Moi, *Bon* 466, May 1881 (p, ♂); Quang Yen Prov., region of Yen Lap, *Chevalier* 37584 (p, ♂). CHINA. Kwangtung: Canton Christian College Campus, *Kwok Yan* 9973 (NY, ♀), *McClure* 13471, May 1925 (K, p, ♀), *To Kang Ping* 11178 (NY, US, ♀), 13898 (A, BM, K, L, p, US, ♀).

Of the three synonyms available to provide an epithet for this subspecies of *Artocarpus nitidus* it seems desirable to choose *A. lingnanensis*, which was described by Merrill in 1931. The two species, *A. parva* and *A. sampor*, that were published simultaneously by Gagnepain in 1926, had somewhat confused descriptions and the second of the species was, furthermore, based on mixed material.

One of the syntypes of *Artocarpus parva*, Balansa 740, bears an abnormal inflorescence with free, tubular perianths, which measures 10×8 mm. This corresponds to the maximum size given by Gagnepain for the male head and is apparently the source of the difference from the measurements given above ($4\text{--}12 \times 3\text{--}4$ mm.). He was also in error in describing and drawing the male perianths as tubular and shortly 4-lobed; in the collection he examined (shown by the sketch attached to the sheet), and in others, the perianths have been found to consist of free segments.

The description of the syncarp of *Artocarpus sampor* was based on Pierre 1637, which consists at Paris, Kew, and Washington of a sterile shoot of *A. nitidus* ssp. *lingnanensis* and a detached syncarp, about 7.5 cm. in diameter with a peduncle 3.5 cm. long, which agrees in its characters with *A. gomezianus* ssp. *gomezianus*. It was presumably the large size of the latter that misled Gagnepain into describing a female head of ssp. *lingnanensis* at anthesis as the male inflorescence (shown by a drawing attached to Fleury 30049), and thus into stating that the male head was globose and 10 mm. in diameter.

ssp. *humilis* (Becc.) Jarrett, stat. nov.

Artocarpus humilis Becc. For. Borneo, 629. 1902; Renner, Bot. Jahrb. 39: 369. 1907. Holotype, Sarawak, Beccari PB 3128 (FI); isotypes (FI, K, P).

Leaves 6–18 \times 1.5–8 cm., elliptic, varying obovate-elliptic, with an acumen to 2.5 cm. long, base cuneate, margin entire; lateral veins 5–9 pairs, curved, ascending; drying red-brown to pale brown, lighter beneath, venation concolorous or straw-coloured. *Male head* 5–6 \times 3–4 mm., obovoid; peduncle 1 \times 1 mm., velutinous. *Syncarp* (submature) to 2 cm. across, drying pale brown, short-pubescent; peduncle 2–20 \times 3 mm., velutinous.

VERNACULAR NAMES: *selangkang*, west Borneo; *betoh*, *tampang*, south and east Borneo.

DISTRIBUTION: in evergreen forest to 3000 ft.; Borneo.

Borneo. SARAWAK. Batan Lupar, Marop, Beccari PB 3128, Mar. 1867 [1866 on label] (FI, K, P, ♂, ♀). WEST BORNEO. Melawi, bb 27034 (BO, L); Pamangkat, Paloh, bb 11345 (BO); Pontianak, Batu Ampar, bb 17421 (A, BO, L, ♀); Simpang, Lubuk Batu, bb 7333 (BO). SOUTH AND SOUTHEAST BORNEO. Sungei Malohapan, Buntok, Lot Obi 2140 (BO, L, ♀). EAST AND NORTHEAST BORNEO. E. Kutei: Loa Djanan, near Samarinda, Kostermans 6363 (K, L, SING), 9953 (L); Tandjong Banko, near mouth of Mahakam River, Kostermans 7129 (L, SING, ♀). W. Kutei: near Muara Kamaw, bank of Mahakam River, Endert

1704 (A, K, L, ♀). BRITISH NORTH BORNEO. Mt. Kinabalu, Dallas, *Clemens* 27571 (BM, K, L, SING, ♀).

As noted in the general discussion of *Artocarpus nitidus*, the length of the peduncle of the female inflorescence in ssp. *humilis* shows considerable variation. In four collections, namely, *Beccari* PB 3128 and *Clemens* 27571 (at anthesis) and *bb* 17421 and *Kostermans* 7129 (submature), the peduncles are about 2 mm. long. In two others, *Endert* 1704 (at anthesis) and *Lot Obi* 2140 (submature), the peduncles are 16–20 mm. long. This variability is not correlated with any other character and, therefore, in view of the rather distinctive appearance of the larger leaves which have markedly curved, ascending veins, all the specimens are at present assigned to a single taxon.

In his description of *Artocarpus humilis*, Beccari stated that the female inflorescence had some unopened male flowers. No such inflorescence has been found on the type collection, the male and female heads being quite normal in appearance, but Beccari was presumably describing one of the abnormal inflorescences quite frequently found in *A. nitidus*.

ssp. *borneensis* (Merr.) Jarrett, stat. nov.

Artocarpus borneensis Merr. Jour. Str. Br. Asiat. Soc. 85: 165. 1922. Holotype, British North Borneo, *Ramos* 1592 (PNH, not seen, photograph in A); isotypes (A, BM, BO, K, L, P, SING).

Leaves 3.5–23 × 1.5–9 cm., elliptic-oblong, varying obovate- or ovate-oblong, attenuate or acuminate, base cuneate or rounded, margin entire; lateral veins 8–15 pairs, curved; drying dark brown to blue-grey above, pale red-brown to greenish beneath, venation concolorous or straw-coloured. *Male head* 3.5–10(–12) × 2.5–7 mm., obovoid or clavate; peduncle 1.5–3 × 2 mm., subappressed-pubescent. *Syncarp* to 6 cm. across, brownish green to purple, drying chestnut- to purple-brown, with a dense indumentum of readily deciduous, clavate, multicellular hairs; peduncle 2–4 × 3 mm., subappressed-pubescent to puberulent.

DISTRIBUTION: in evergreen forest to 5000 ft.; Borneo.

Borneo. SARAWAK. 12 mile Penurision road, *Egon* A 0921 (KEP, ♀). EAST AND NORTHEAST BORNEO. Balikpapan: Gunong Beratus, *Kostermans* 7365 (K, L, PNH, ♀). W. Kutei: near L. Petah, *Endert* 3191 (A, L, SING, ♂, ♀). BRITISH NORTH BORNEO: Mt. Kinabalu, Dallas, *Clemens* 26350 (A, BM, BO, K, L, NY, ♀); Mt. Kinabalu, Gurulau Spur, *Clemens* 50472 (A, BM, K, L, ♀); Penibukan, *Clemens* 31233 (A, BM, K, L, NY), 40504 (BM, K, ♀); near Sandakan, *Ramos* 1592 (A, BM, BO, K, L, P, SING, ♀); Sandakan, Batu Lima, *Ramos* 1749 (A, BO, K, P, SING, ♂, ♀).

The following collections are referable either to ssp. *borneensis* or to ssp. *griffithii*.

Borneo. SARAWAK. Kuching, Semengoh For. Res., *Herb. Sar. Mus.* 7728 (K, L, ♂); Saribas, Pakeo, *Haviland & Hose* 3315 (A, BM, K, L, ♂). WEST BORNEO. Ketapang, Muara Kajan, Sungei Kelilo, *bb* 7460 (BO); Palo, *Becking* 44 (BO).

SOUTH AND SOUTHEAST BORNEO. Martapura, Kalaan, *bb* 12054 (BO); Pleihari, Kintap, *bb* 7759, 7761 (BO); Sampit, Sansang, *bb* 10538 (BO). EAST AND NORTH-EAST BORNEO. Berouw: Tandjong Redeb, Labanan, *bb* 11508 (BO). E. Kutei: Sg. Tiram, *bb* 35021 (K, L, abnormal infl.). W. Kutei: Tandjong Isui, *Enderit* 1954 (K, L).

ssp. *griffithii* (King) Jarrett, comb. et stat. nov.

Artocarpus gomeziana Wall. var. *griffithii* King in Hook. f. Fl. Brit. Ind. 5: 544. 1888; King, Ann. Bot. Gard. Calcutta 2: 16. t. 14B. 1889. Syntypes, Malaya, *Griffith* 4665, *King* 6651, 7533, *Scortechini* 683 (CAL, not seen; duplicates examined, K, SING, etc.).

Artocarpus eberhardtii Gagnep. Bull. Soc. Bot. Fr. 73: 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 737. 1928. Holotype, Annam, *Eberhardt* 3288 (P).

Artocarpus eberhardtii Gagnep. var. *poilanei* Gagnep. Bull. Soc. Bot. Fr. 73: 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 737. 1928. Syntypes, Laos, *Poilane* 11777, 11955 (P); lectotype, *Poilane* 11955 (P).

Artocarpus griffithii (King) Merr. Pap. Mich. Acad. I. 24: 64. 1939.

Artocarpus gomezianus auct. non Tréc., King, Ann. Bot. Gard. Calcutta 2: 15. 1889, pro parte, quoad t. 14A et spec. *King* 4189, 5078, 7535, 8838; Renner, Bot. Jahrb. 39: 368. 1907; Ridley, Fl. Malay Penin. 3: 355. 1924; Corner, Wayside Trees, 654, t. 195. 1940; Watanabe, Ic. Econ. Pl. S. Asia, 528. 1945.

Artocarpus lanceolata auct. non Tréc., Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 738. 1928.

Differs from ssp. *borneensis* as follows: *syncarp* orange-pink with bright pink flesh, or yellow, nigrescent on drying, glabrous or with sparse rufous hairs; peduncle 3–5 (–15) mm.

VERNACULAR NAME: *tampang* (Malay), Malaya and Sumatra. USES: the *syncarp* is edible.

DISTRIBUTION: in evergreen forest to 5000 ft.; peninsular Siam, Indochina, Yunnan.

Siam. PENINSULAR SIAM. Kantang, *Haniff & Nur* 3298 (SING, ♀); Pattani, Toh Moh, *Kerr* 584 (BM, ♂). INDOCHINA. CAMBODIA. Kampot Prov.: Cam Chay Mts., near Kampot, *Pierre* 4696 (A, BM, K, P, ♀). Pursat Prov.: near Trassay, *Poilane* 15094 (P, ♀). ANNAM. Thu Thien Prov.: near Huê, *Eberhardt* 3288 (P, ♂). LAOS. Savannaket, *Poilane* 11777, Jan. 1925 (K, P, ♂), 11955, Feb. 1925 (P, ♂); Tatom, Chieng Kwang, *Kerr* 20844 (BM, K, ♂); upper Tchépone and Quangtri River, *Poilane* 13524 (A, P, ♀). CHINA. YUNNAN. Che-li Hsien, *Wang* 78652 (A, ♀); Fo-hai, *Wang* 77124 (A, ♂).

Malaya. KEDAH. Katumbah, *Boswell* KEP 12581 (KEP, ♀); Kuala Muda, *Ali* KEP 73794 (KEP, ♀); Semling, Kedah Peak, *Bell & Haniff*, Mar. 1911 (K, ♂, ♀). PROV. WELLESLEY. *Ridley* 12624 (BM, ♀). PERAK. *King* 6651, Sept. 1884 (SING, ♀), *Scortechini* 683 (K, SING, ♀), 1837 (K, ♂); 14 miles Bruas, *Hashim* KEP 207 (KEP, ♀); Larut, *King* 4189 (K, ♀), 5078 (K, P, SING, ♀), 7533, Apr. 1885 (BM, CGE, K, P, SING, ♀), 7535 (BM, K, SING, ♀); Matang, Jamba, *Wray* 2520 (SING, ♀); Taiping Hill, *Haniff* SFN 13201, *Ridley* 11393 (K, SING, ♀); Ulu Selangor, *King* 8838 (K, L, ♀); Waterfall Hill, *Wray* 2073 (SING, ♀). DINDINGS. Bruas, *Murdoch* 207 (SING, ♀). KELANTAN. *Walton*

KEP 32682 (KEP). TRENGGANU. Kemaman, *Corner SFN 30568* (SING, ♀). PAHANG. Kuantan: Bukit Belai, Betinbang Chini, *Lambak CF 2716* (κ, SING, ♀); Bukit Sembambu, *Soh KEP 15742* (KEP, ♂, ♀). SELANGOR. Ampang For. Res., *Strugnell KEP 12720* (KEP, ♀); Bukit Kulu, *Goodenough 10535* (CAL, SING, ♀); Kanching, *Symington CF 20192* (SING); Kepong, *Murdoch 314* (BM, ♀); Kepong, Bukit Lagong For. Res., Sungei Kroh, *Sinclair SFN 40120* (KEP, L, ♂); Klang Gate, *Murdoch 94* (BM, ♀); Kuala Lumpur, *Curtis 2386* (BM, SING, ♀); Kuala Lumpur, Carcosa Domain, *Foxworthy 10944* (SING, ♂); Kuala Lumpur, Public Gardens [? planted], *Ahmad CF 3034, 4986* (κ, SING, ♂, ♀), *Omar CF 8872* (κ, SING, ♀), Kuala Lumpur, Weld Hills For. Res., *Hashim CF 3002* (κ, SING, ♀); 20th mile Pahang road, *Ridley 8466* (SING, ♂). NEGRI SEMBILAN. Bukit Kaju Arang, *Alvins* (SING); Bukit Payong, *Alvins 772* (SING); Nilai Jindaram Estate, *Shah 65* (κ, L, ♂); Tampin, Kuala Pila road, *Nur SFN 2814* (κ, ♂); Tampin, Seremban road, *Nur SFN 1414* (κ, SING, ♀). MALACCA. *Griffith 4662* (κ, P, ♀), *4665, 1845* (GH, κ, P, ♂, ♀), *s.n.* (CGE, κ, ♂, ♀), *Maingay 1482* (κ, ♂, ♀); Brisu, *Derry 551* (P, SING, ♀); Bukit Bruang, *Derry 435* (SING, ♀); Bukit Senggeh, *Goodenough 1835* (BM, SING, ♀); Panchor, *Goodenough 1667* (SING, ♀); Selandar, *Alvins 246* (SING, ♀); Sungei Udang, *Alvins 1* (SING, ♀); 14th mile Sungei Udang For. Res., *Sinclair SFN 40565* (κ, SING, ♀); N. Sunklar, *Alvins 58* (SING, ♀). JOHORE. 7th mile Kota Tinggi-Mawai road, *Corner SFN 21349* (A, BM, BO, κ, SING, ♂, ♀). PENANG. Government Hill, *Curtis 657* (κ, SING, ♂, ♀); Penara Bukit, *Curtis 1201* (κ, SING, ♀). SINGAPORE. *Hullett 16* (SING), *Marton 90* (κ, ♂); Changi, *Ridley 4832* (SING, ♀).

Sumatra. ATJEH. Gajo Lueus, Penosan, Gunong Gerupal, *bb 22364* (A, BO, L). TAPANULI. Angkola and Sipirok, Panobasan, *bb 25248* (A, BO, L, ♀). WEST COAST. Mt. Sago near Pajakumbuh, *Meijer 4056a* (L, ♀ and abnormal infls.), *4746* (L, abnormal infls.); Painan, Barung Balantai, *NIFS SWK/I-15* (BO). EAST COAST. Asahan: Aek Munte, *Rahmat si Boeea 9293* (A, L, ♀); Huta Padang, *Krukoff 4372* (A, BO, NY, SING, ♀); near Lumban Ria, *Rahmat si Boeea 7514, 8042* (A, L, SING, ♀). PALEMBANG. *Praetorius* (L); Banjuasan and Kubustreken, Bajunglintjir, *NIFS T 704* (BO, L, U, ♂, ♀); Lematang Ilir, Gunong Megang, *NIFS T 808* (BO, L, ♀); Muara Dua, Kisau, *bb 9231* (BO).

Borneo. SARAWAK. Kuching, 6th mile For. Res., *Herb. Sar. Mus. 9436* (κ, L, ♀). EAST AND NORTHEAST BORNEO. E. Kutei: Samarinda, Loa Djanan region along road to Balikpapan, *Kostermans 10202* (κ, ♀).

In describing *Artocarpus gomezianus* var. *griffithii*, on which ssp. *griffithii* is based, King failed to distinguish accurately between the type and his variety, although the latter differs clearly in the shorter petioles and peduncles, the smaller, narrower male head, and the glabrous syncarp. King's description of *A. gomezianus* [ssp. *gomezianus*] was partly based on specimens which should have been referred to the variety and the illustration (*t. 14A*) was drawn from one of these. In consequence the two entities were not distinguished by later authors and Malayan collections of both were identified as *A. gomezianus*. Merrill, in 1939, realized that they should be assigned to two distinct species, and raised var. *griffithii* to specific rank, without, however, noting any affinity between it and *A. borneensis*, described by him in 1922.

Artocarpus nitidus ssp. *griffithii* is considerably more common and

widely distributed in Malaya than *Artocarpus gomezianus* ssp. *gomezianus*, and the descriptions under *A. gomezianus* given by Ridley (1924) and Corner (1940) are based solely on ssp. *griffithii*.

Several specimens of ssp. *griffithii* from peninsular Siam, the northern part of Malaya, and Penang have syncarps with rather long peduncles (to 15 mm.), but they otherwise agree well with the rest of the collections assigned to this subspecies. The edible ripe syncarp is described in Malaya as orange-pink with bright pink flesh (fide Corner, 1940, and various field notes), but in Indochina the notes on several collections state that it is yellow. In spite of evidence in this species, as in *A. fretessii*, of some confusion with the male inflorescences, there appears to be a genuine difference in colour. No further information is available concerning the precise distribution of the two variants, but, according to present evidence, the pink form occurs south and the yellow form north of a discontinuity in the distribution of the subspecies between peninsular Siam and Indochina.

Series *Clavati* Jarrett, ser. nov.

Inflorescentiae bracteis interfloralibus clavatis vel spathulatis. *Capitula mascula* cellis antherum 0.3–0.5 mm. longis.

TYPE SPECIES: *Artocarpus hypargyreus* Hance.

44. *Artocarpus petelotii* Gagnep. Bull. Soc. Bot. Fr. 73: 89. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 739. 1928. Holotype, Tonkin, *Petelot s.n.* (P).

Artocarpus brevisericea C. Y. Wu & W. T. Wang, Acta Phytotax. Sin. 6: 273. t. 55, fig. 22. 1957. Holotype, Yunnan, *Exped. Biol. Sino-ross. ad prov. Yunnan 1196* (PE ?, not seen); isotype (A).

Trees, height to 10 m. *Twigs* 3–4 mm. thick, pubescent, hairs white or rufous, patent, straight. *Leaves* 9–23 × 4–9 cm., elliptic to narrowly elliptic, with an acumen to 1.5 cm. long, base cuneate, margin entire or denticulate towards the apex; main veins and reticulum prominent beneath; glabrous above except for the pubescent main veins, venation beneath moderately to thinly pubescent, hairs rufous or colourless, straight; lateral veins 7–11 pairs, curved, ascending; intercostals few, parallel; drying grey-green or dingy brown, paler beneath, venation concolorous or straw-coloured; petiole 13–18 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 18–23 × 5–7 mm. (fide Wu & Wang, 1957), narrowly obovoid; perianths of 2 or 3 spathulate, free segments 0.8 mm. long; stamen (not exerted), anther-cells oblong, 0.35 mm. long; bracts stoutly to slenderly stalked, heads spathulate, secund, to 0.7 mm. across, these and perianths densely pubescent; peduncle 5–10 mm. long (fide Wu & Wang, 1957), greyish pubescent; *female head* irregularly rugose and papillate, with the styles exerted to 1.5 mm. through low papillae (2–)3(–4)-fid at the apex,

and longer, cylindric papillae projecting to c. 1.5 mm. scattered on the surface between these. *Syncarp* to 3 cm. across, subglobose, shallowly lobed, drying rufous, pubescent, smooth over the lobes, the surface between papillate, the longer papillae mostly broken off; wall c. 2 mm. thick; proximal region of perianths fused above, walls double and separable below, fruiting perianths 1-8(?), slightly fleshy, "seeds" (pericarps with a horny endocarpic layer) ellipsoid, 13×10 mm.; core c. 5 mm. across; peduncle $35-40 \times 3$ mm., pubescent.

DISTRIBUTION: in forest to 6000 ft.; Tonkin and Yunnan.

Indochina. TONKIN. Chapa, *Petelot* 6028 (A, P, ♀); [probably Cho-ganh, fide Gagnepain, 1926] *Petelot* (P, ♀). China. YUNNAN. Chin-ping, Ho-tou-chai, *Exped. Biol. Sino-ross.* 1196, May 1956 (A, ♂).

The two collections of *Artocarpus petelotii* from Tonkin bear female inflorescences; these are at anthesis on the holotype and mature or nearly so on *Petelot* 6028 (collected in 1930). The styles are exerted through low papillae with lobed apices, but between these the surface bears, in addition, numerous larger, irregular papillae. The presence of the latter, and the complete absence of discoid peltate bracts indicates an affinity with the two other species assigned to series *Clavati*, rather than with any member of series *Peltati*, although the leaves are patent-pubescent beneath instead of tomentulose, as in these two species.

The recent collection cited from Yunnan bears male inflorescences and shows a strong vegetative resemblance to the Indochinese specimens, apart from a difference in the colouration when dried, which will be discussed below. This collection was described in 1957 as *Artocarpus brevisericea* by Wu and Wang, who compared it with *A. hypargyreus*, but made no mention of *A. petelotii*. They noted that the interfloral bracts in the male inflorescence differed in shape from the clavate bracts found in *A. hypargyreus*, but described them incorrectly as peltate, and thus presumably regarded them as similar to the bracts of *A. ficifolia* (= *A. lakoocha*), published by Wang in the same paper (A preliminary report on the study of the tropical and subtropical flora of Yunnan I. *Acta Phytotax. Sinica* 6: 267-300. t. 55. 1957). The heads of the bracts are not, however, discoid and centrally attached, with a ciliate margin, as in *A. lakoocha* and other members of series *Peltati*, but spatulate and secund, with a densely pubescent upper surface. In the smaller, slenderly stalked bracts the shape is easily observable, but it is somewhat obscured by the pubescence in the scattered, larger, stoutly stalked bracts. Thus, in the shape of the interfloral bracts this collection, also, shows an affinity with the other species of series *Clavati*, an affinity which is confirmed by the large size of the anthers (fully developed in the inflorescences on the isotype at the Arnold Arboretum, although not yet exerted).

The three collections resemble each other closely in the shape and venation of the leaves, and in the type and distribution of the indumentum, which consists of patent hairs having a rather broad lumen, especially on the twigs. However, whereas in the isotype of *A. brevisericea* the hairs

are colourless or whitish, giving a greyish tinge to the specimen, and the leaves dry grey-green, in the Petelot collections most of the hairs are rufous, though some are colourless, and the leaves dry a dingy brown. The latter colouration is abnormal for this series, since both *A. hypargyreus* and *A. styracifolius* dry grey or grey-green, with a greyish pubescence, and it is perhaps an artifact due to the method of drying.

In view of the vegetative similarity of the three collections except in their colour when dried, and the general agreement of the characters of both the male and the female inflorescences with those of the other members of series *Clavati*, it is assumed that only a single species is represented, and *A. brevisericea* is therefore reduced to *A. petelotii*.

45. *Artocarpus hypargyreus* Hance in Benth. Fl. Hongkong. 325. 1861, "*hypargyrea*"; Chung, Mem. Sci. Soc. China 1: 33. 1924; Walker, Lingnan Sci. Jour. 6: 51. 1930; Merr. ibid. 13: 56. 1934; Lee, For. Bot. China, 444. t. 125. 1935; Herklots, Hongkong Countryside, 153. 1951. Holotype, Hongkong, *Hance* 4484, June 1859 (κ); isotype (BM).

Evergreen trees, height to 10 m., bark dark purple, peeling off in flakes. *Twigs* 1.5–2 mm. thick, finely rugose, greyish or rufous subappressed-pubescent. *Leaves* 8–17 × 4–8 cm., elliptic to obovate- or oblong-elliptic, acuminate, base cuneate, margin entire; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; glabrous above except for the puberulent midrib, venation beneath appressed-puberulent, glabrescent, intervenium minutely tomentose; lateral veins 7–9 pairs, curved; intercostals parallel or reticulate; dark green above, grey-green or whitish beneath, drying greyish above, greyish glaucous beneath from the tomentum, the main veins nigrescent; petiole 10–20 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 15–20 × 10–15 mm., obovoid to clavate; perianths of c. 4 linear or spatulate free segments 1 mm. long; stamen 1.2 mm. long, filament cylindric, anther-cells ellipsoid, 0.3 mm. long; bracts slenderly stalked, heads clavate, to 0.3 mm. across, these and perianths densely and minutely pubescent; peduncle 10–23 × 1 mm., shortly greyish pubescent; *female head* with the surface papillate and the styles exerted to 0.5 mm. through perforations between the papillae. *Syncarp* (submature) to 2 cm. across (the size of an apricot, fide Herklots, 1951), subglobose, yellow or apricot with reddish orange flesh, drying brown, pubescent, nearly smooth, papillae persistent but inconspicuous; proximal region of perianths free, fruiting perianths c. 12 (fide Herklots, 1951); peduncle 35–50 × 2.5 mm., short-pubescent.

VERNACULAR NAMES: *hung kwai muk*, *kwai muk*.

DISTRIBUTION: in forests and open woods, southern China (Kwangtung, Hainan, Hongkong).

China. KWANGTUNG. Lochang district, Yao Shan, Tau Kung, *Tso* 20851 (A,

K, P, SING, ♂, ♀); Sin-fung district, Hau T'ong Shan, Fuk Lung Monastery, *Taam* 885 (A, ♀); Sin-fung district, Sha Lo Shan, Lo Lo Ha, *Taam* 929 (A, ♀); Tapu district, Tai Mo Shan, *Tsang* 21182 (A, K, P, ♀). HAINAN. *Ford* (A, ♀); Ching Mai district, Pak Shik Ling, Ku Tung village, *Lei* 448 (A, K, L, NY, P, SING, ♂); Taam Chau district, Hung Shek Shan, *Tsang* 16850 (A, K, ♂). HONGKONG. *Chun* 40037 (NY, ♂), *Hance* 4484, June 1859, and 1878 (BM, K, ♂, ♀), *s.n.* (GH, K, ♂, ♀); Aberdeen New Road, near Little Hongkong, *Chun* 7460 (NY, ♀), *Gibbs* 7473 (A, ♂); Mt. Gough, *Bodinier* 1208 (P, ♀); Pokfoolung stream, *Esquirol* 1167 (P, ♂, ♀); Shuitong Road near Peak, *Taam* 2259 (A, US, ♂, ♀); Ty-tam-took, *Lamont* 696 (BM). Cultivated. CHINA. Hongkong, *Hert. Bot.*, *Fond*, July 1880 (K, ♀).

The surface of the syncarp in *Artocarpus hypargyreus* is papillate between the perforations through which the styles are exerted at anthesis. By analogy with the structure of the male inflorescence, it is assumed that in this species, and also in *A. petelotii*, the papillae are formed by the heads of interfloral bracts.

Artocarpus hypargyreus is readily distinguished from *A. styracifolius* when sterile by the broader leaves having a slightly prominent reticulum, and by the stouter, pubescent twigs. It may be noted that the western Malaysian *A. glaucus*, which resembles these two species in having a minute tomentum on the under surface of the leaf, although it is not closely related, can be distinguished by the more numerous lateral veins (8–15 vs. 4–9 pairs), in addition to the inflorescence characters. Fernandez-Villar recorded *A. hypargyreus* incorrectly from the Philippines (Noviss. App. 203. 1880).

46. *Artocarpus styracifolius* Pierre, Bull. Soc. Bot. Fr. 52: 492. 1905, "*styracifolia*"; Gagnep. in Lecomte, Fl. Gén. Indoch. 5: 733. 1928; Wu & Wang, Acta Phytotax. Sin. 6: 272. 1957. Holotype, Laos, *Spire* 344 (P); isotypes (P).

Artocarpus bicolor Merr. & Chun, Sunyatsenia 1: 52. 1930; Chun in Hu & Chun, Ic. Pl. Sin. 4: 6. t. 156. 1935, descr. addend.; Merr. Lingnan Sci. Jour. 11: 41. 1932; McClure, ibid. 13: 586. 1934. Holotype, Kwangtung, *Wang & Ling* 7409 (UC, not seen); isotypes (BM, K, P; K and P both as *Wong* 7409).

Trees, height to 20 m., bark dark grey, rough. Twigs 1–1.5 mm. thick, finely rugose, appressed-puberulent, soon glabrescent. Leaves 4–11 × 1.5–4 cm., elliptic to obovate-elliptic, with an acumen to 1.5 cm. long, base cuneate and decurrent, margin entire; juvenile leaves pinnatifid; main veins only prominent beneath; glabrous above, main veins appressed-puberulent beneath, glabrescent, intervenium minutely tomentose; lateral veins 4–8 pairs, curved; intercostals few, reticulate; deep green above, pale green or glaucous beneath, drying greyish green above, greyish glaucous beneath from the tomentum, the midrib reddish or nigrescent; petiole 6–12 mm. long.

Inflorescences solitary in leaf-axils. At anthesis: male head 6–12 × 4–7 mm., ellipsoid, obovoid or cylindric; perianths 2–3-lobed above,

1.3 mm. long; stamen 2.5 mm. long, filament slender, slightly tapered above, anther-cells oblong, 0.5 mm. long; bracts slenderly stalked, heads clavate, to 0.2 mm. across, these and perianths minutely pubescent; peduncle $5-13 \times 1$ mm., velutinous; *female head* with numerous flexuous cylindric processes and the styles exerted to 0.5 mm. through perforations in the surface between these. *Syncarp* to 4 cm. across, globose, yellow, drying red-brown, pubescent, bearing numerous flexuous, cylindric processes to c. 5×0.5 mm.; wall c. 2 mm. thick; proximal region of perianths fused, fruiting perianths to c. 6, thin-walled, "seeds" (pericarps with a horny endocarpic layer) globose, c. 10 mm. across; core c. 5 mm. across; peduncle $(10-18-25) \times 2$ mm., velutinous.

DISTRIBUTION: in thickets and forests to 4000 ft., often in dry localities, northern Indochina, southern China.

Indochina. LAOS. Phoutane, *Spire* 334 (P, ♀); upper Tchépone, *Poilane* 12219 (P, ♂). TONKIN. Pac-si, ne. of Mon-cay, *Tsang* 26970 (A, ♀); Tien Yien, *Fleury* 37946 (P). CHINA. YUNNAN. Si-chour-hsien, Ting-mann, *Feng* 12296 (A, ♂, ♀). KWEICHOW. Sanhoa, *Tsiang* 6350 (A, K, ♂). KWANGSI. N. Lin Yen, Tsin Lung Shan, *Ching* 6950 (A, NY, ♂, ♀); W. Poseh, Bako Shan, *Ching* 7654 (A, NY, US, ♂); Sup-man-ta Shan, *Liang* 69783 (A, ♂, ♀); Tou Ngok Shan, *Tsang* 23151, 23259 (A, P, ♀). KWANGTUNG. Fang Ch'eng district, Kung P'ing Shan, T'aan Faan, *Tsang* 26803 (A, ♂); North River, *Wang & Ling* (or *Wong*) 7409, Nov. 1928 (BM, K, P, ♀); Poon Yue district, *Levine* 3158 (A, ♀); Wang Yuen district, Fan Shiu Shan, near Fan Shiu Au, *Lau* 2296 (A, ♀); Wang Yuen district, Tsing Wan Shan, near Wong Chuk Island, *Lau* 2196 (A, ♂); Ying Tak, *Wang* 30010 (BM, ♀). HAINAN. *Liang* 62258 (A, ♂, ♀), 65506 (NY); Ah Ping, *Chung & Tso* 43998 (A, NY, US, ♂); Dai Land, Dung Ka, *Chun & Tso* 43895 (A, K, P, ♀); Hung Mo Tung, *Shing* 816 (NY); Po-ting, *How* 73288 (A, BM, P, ♂), 73505 (A, BM, P, ♀); Yiachow, *Liang* 62258 (K, ♂).

Artocarpus styracifolius is unique among the species of subgenus *Pseudojaca* in that the syncarp is covered by flexuous processes. These have been mistaken by all previous authors for the elongate apices of perianths, but the styles can be seen to be exerted through perforations in the surface between the processes, and the latter apparently represent hypertrophied interfloral bracts (see the introductory paper for a discussion of their morphology, Jour. Arnold Arb. 40: 15. fig. 4b. 1959). In the male inflorescence the bracts are clavate, as in *A. hypargyreus*. The small, elliptic, acuminate, glaucous leaves are also very distinctive in their appearance.

In 1957, Wu and Wang reduced *Artocarpus bicolor* Merr. & Chun, under which name this species had been known previously in China, to *A. styracifolius*. These authors also cited the following collections from Yunnan, which have not been seen in the course of this study: *P. I. Mao* 538, 551, 2356, 3066, 5416, 12296; *Wang* 85909, 86018, 86028.

Section *Glandulifolium* Jarrett, sect. nov.

Folia margine glandulifera. *Capitula* feminea stylis bifidis.

TYPE SPECIES: *Artocarpus altissimus* (Miq.) J. J. Smith.

47. *Artocarpus altissimus* (Miq.) J. J. Smith, Ic. Bogor. 3: 79. *t.* 233. 1907, "*altissima*"; Douglas & Baas Becking, Bull. Jard. Bot. Buitenzorg III. 17: 291, 297. *t.* 10. 1947.

Morus ? *altissima* Miq. Fl. Ind. Bat. Suppl. 415. 1861. Syntypes, Sumatra, *Teysmann HB 3903, 3972* (L); lectotype, *Teysmann HB 3972* (L).

Grewia ? *subcordata* Miq. Fl. Ind. Bat. Suppl. 404. 1861; Burret, Notizbl. Bot. Gart. Berlin 9: 736. 1926. Syntypes, Sumatra, *Teysmann HB 3734, 4042* (L); lectotype, *Teysmann HB 4042* (L).

Artocarpus altissima Teysm. & Binnend. Cat. Hort. Bog. 85. 1866, nomen nudum.

Deciduous trees, height to 30 m., stoutly buttressed, bark brown, peeling off in long flakes. *Twigs* 1.5–3 mm. thick, shallowly rugose, short-pubescent, soon glabrescent. *Leaves* 6–15 × 5–10 cm., ovate to ovate- or obovate-oblong, acuminate, base usually shallowly cordate, margin glandular-crenate; juvenile leaves with 1–2 pairs lateral lobes; main veins and intercostals prominent beneath, reticulum slightly so; puberulent above with the main veins short-pubescent, rather thinly pubescent on the venation beneath, glabrescent; lateral veins 5–9 pairs, straight, basal pair usually rather strongly developed and leaf base hence trinerved; intercostals parallel, basal tertiaries strongly developed; green (turning orange-yellow on the tree), drying blue-grey to brown above, paler brown beneath; petiole 10–25 mm. long, often geniculate at the junction with the lamina.

Inflorescences axillary on short-shoots borne on older wood before the new leaves appear. *At anthesis: male head* 5–8 × 2–3 mm., ellipsoid or cylindric; perianths of 4 free segments 0.7 mm. long, puberulent; (stamen not exerted), anthers oblong, 0.4 mm. long; bracts slenderly stalked, heads peltate, to 0.6 mm. across, ciliate; peduncle 5–7 × 0.5 mm., velutinous; *female head* 5 mm. across, globose, the surface velutinous, with deeply bifid styles exerted to 1 mm. through papillae, and numerous peltate bracts; proximal region of perianths fused; peduncle to 12 × 2 mm., velutinous. *Syncarp*

VERNACULAR NAME: *klutum*, Sumatra.

DISTRIBUTION: in evergreen forest to 1800 ft.; Sumatra, west Borneo.

Sumatra. ATJEH. Langsa, A. Tjanang, *bb 14504* (BO). TAPANULI. Angkola and Sipirok, *bb 5626* (BO, L). EAST COAST. Simelungun, G. Maligas, *bb 20436* (BO, L). PALEMBANG. Heyne (BO, L, ♂, ♀), *Praetorius* (L); Batu Radja, *Teysmann HB 3734* (BO, L); Muara Dua, *Teysmann HB 3903* (BO, L); Muara Enim, *Teysmann HB 4042* (BO, L); Sekaju Munie, *Teysmann HB 3972* (BO, L). LAMPONGS. Kebang, *Teysmann HB 4214* (BO, L). BORNEO. WEST BORNEO. Sanggau, *bb 18789* (BO, L). Cultivated. JAVA. Bogor, Hort. Bot., *HB 7241* (BO), *VIII B 46* (L).

The material available of *Artocarpus altissimus* is inadequate for the preparation of a full description of the species. The type is sterile, as are all the other collections cited, except for one made by Heyne in

Palembang which has inflorescences at anthesis. These agree with the description, based on material from two trees in the Hortus Bogoriensis, that was published by J. J. Smith in transferring Miquel's *Morus altissimus* to *Artocarpus*. Smith stated that the syncarps did not mature on these trees, but I am informed by Mr. E. J. H. Corner that he found fruit on them containing seeds measuring c. 7×5 mm. The germination of these was characteristic of *Artocarpus*, since the cotyledons remained enclosed in the seed-coat, while the epicotyl lengthened and the first pair of foliage leaves were opposite, the subsequent ones being arranged spirally.

The specimens match closely in their vegetative characters, which are aberrant for the genus in several respects. The leaves are palmately tri-nerved at the base, usually with a strong development of the basal tertiary veins, and the petiole is frequently geniculate at the junction with the lamina. The margin is crenate-dentate, with evenly spaced patches of glandular tissue lying at the end of short nerves running out to the edge of the leaf. These patches are present in addition to the glandular hairs with unicellular heads that are characteristic of subg. *Pseudojaca*. The leaves have a superficial resemblance to some members of the Tiliaceae, and Miquel described another collection as *Grewia subcordata*, which was reduced to *Artocarpus altissimus* by Burret in 1926.

The inflorescence characters are, nevertheless, those of *Artocarpus*, although the long-exserted, deeply bifid styles are again unusual, at least for subg. *Pseudojaca*. The tree is deciduous and the inflorescences are borne on short-shoots before the new flush of leaves appears. Smith, however, shows a young leaf with a crenate margin attached to the shoot-bearing inflorescences. These shoots are entirely leafless on the Heyne collection, but very young leaves dissected from the buds appear to show the glandular margin, while the twigs and buds agree with those of leafy shoots.

This species thus appears to be correctly described and referred to *Artocarpus*. In the more or less distichous arrangement of the leaves on the ultimate twigs, and the nonamplexicaul stipules, as well as in the size and shape of the inflorescences and the completely divided male perianth, *A. altissimus* agrees with subg. *Pseudojaca*. However, there is no obvious affinity with any other members of the subgenus and, in view of the very aberrant vegetative characters, the species is assigned to a separate section *Glandulifolium*.

SPECIES EXCLUDENDAE ⁵

ARTOCARPUS (?) AFRICANA Sim, For. Fl. Port. E. Africa, 102. t. 32. 1919 (holotype, Mozambique, Sim 5999 (PRE, not seen)) = *Treculia* cf. *africana* Dcne ex Tréc. Ann. Sci. Nat. Bot. III. 8: 109. 1847.

⁵ The concluding portion of this paper refers to the genus *Artocarpus* as a whole, i.e., to this and the preceding paper, Studies in *Artocarpus* and allied genera, III. A revision of *Artocarpus* subgenus *Artocarpus*. Jour. Arnold Arb. 40: 113-155, 298-368. 1959.

ARTOCARPUS BRACTEATA King in Hook. f. Fl. Brit. Ind. 5: 540. 1888; King, Ann. Bot. Gard. Calcutta, 2: 7. t. 1B. 1889 = *Parartocarpus bracteatus* (King) Becc.

ARTOCARPUS CANARANA Miq. Verh. Ned. Inst. III. 5: 20. 1852 (holotype, Kanara, near Mangalore, *Hohenacker 796a* [leg. Metz] (u); isotypes (c, k, l, p)) = *Hopea wightiana* Wall. ex Wight & Arn. Prodr. 85. 1834. Metz' collection bears echinate insect galls that were mistaken by Miquel for the male inflorescences of *Artocarpus*. In describing this specimen as *A. canarana* he erroneously suggested that it might be the same as *A. lanceifolius* Roxb. (a species of western Malaysia described from Penang). The latter determination appeared on the herbarium labels and Thiselton Dyer, who cited the collection correctly under *Hopea wightiana* in the "Flora of British India" (1: 309. 1874), quoted only this identification, on Miquel's authority, without mention of *A. canarana*. This is the origin of the statement by Watt (Dict. Econ. Prod. India 4: 273. 1890), followed by Cooke (Fl. Bombay 1: 86. 1903), that Roxburgh had described the galls of *Hopea wightiana* under the name *Artocarpus lanceifolius*. The same galls were the basis of the name *A. ponga* Dennst., and they are commented on further below.

ARTOCARPUS CANNONI W. Bull in T. Moore, Florist & Pomol. 1875: 210. 1875; Van Houtte, Fl. Serres 21: 131. tab. 1875 = *Ficus cannonii* (W. Bull) N. E. Brown, Gard. Chron. III. 3: 9. 1888, "*canoni*"; Solereder, Bull. Herb. Boiss. II. 3: 515. t. 3. 1903. See below under *Artocarpus laciniata* Veitch.

ARTOCARPUS CERIFERA Miq. Ann. Mus. Lugd.-Bat. 3: 212. 1867 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS ELONGATA Miq. Fl. Ind. Bat. Suppl. 419. 1861, Ann. Mus. Lugd.-Bat. 3: 213. 1867 (holotype, Sumatra, Sibolga, *Teysmann HB 767*) = *Sloetia elongata* (Miq.) Koord. Exkursionsfl. Java 2: 90. 1912.

ARTOCARPUS EXSCULPTA W. Bull, Gard. Chron. II. 10: 84. t. 11. 1878 (*Ficus exsculpta* in ind.) = *Ficus exsculpta* W. Bull, Cat. no. 154, 5. t. 1. 1879. This species was mentioned briefly in the Gardeners' Chronicle of 1878 as having been exhibited recently by W. Bull at Preston under the provisional name of *Artocarpus exsculpta*. The figure given of a sterile shoot closely resembles the plate of a fertile shoot of *Ficus exsculpta*, which appeared as new introduction from the South Sea Islands in Bull's Catalogue for 1879. The latter was also stated to have been exhibited at Preston, and the names may be assumed to refer to the same plant. This is supported by the apparent correction in the index of the Gardeners' Chronicle.

ARTOCARPUS FORBESII King in Hook. f. Fl. Brit. Ind. 5: 539. 1888; King, Ann. Bot. Gard. Calcutta 2: 7. t. 1A. 1889 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc. ssp. *forbesii* (King) Jarrett.⁶

ARTOCARPUS FRUTESCENS Renner, Bot. Jahrb. 39: 367. 1907 = *Prainea frutescens* Becc.

ARTOCARPUS INVOLUCRATA K. Schum. in Schum. & Holtr. Fl. Kais. Wilhelmsland, 39. 1889 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS LACINIATA Veitch, Gard. Chron. II. 4: 159. 1875; Solereder, Bull. Herb. Boiss. II. 3: 515. t. 3. 1903 = *Ficus cannonii* (W. Bull) N. E. Brown,

⁶ This footnote is to draw attention to the new combination which it is necessary to make here: *Parartocarpus venenosus* (Zoll. & Mor.) Becc. ssp. *forbesii* (King) Jarrett, comb. et stat. nov.; basionym *Artocarpus forbesii* King, Ann. Bot. Gard. Calcutta 2: 7. t. 1A. 1889.

Gard. Chron. III. 3: 9. 1888. Both *Artocarpus laciniata* and *A. cannoni* were introduced as seedlings from the Society Islands. They were valued for their dissected, brightly coloured leaves and the two species were based on differences in these. On flowering both proved to be figs and Solereder, who studied them in some detail, showed that they were conspecific, agreeing in characters of the fig and of leaf anatomy. The dissected leaves were juvenile forms, whereas the adult leaves were entire. Solereder considered that the differences in leaf colour between the two species and a variety of *A. laciniata*, described by Veitch as *A. laciniata metallica*, might be due to cultural conditions.

ARTOCARPUS LIMPATO Miq. Fl. Ind. Bat. Suppl. 421. 1861 = *Prainea limpato* (Miq.) Beumée ex Heyne.

ARTOCARPUS PAPUANUS Renner, Bot. Jahrb. 39: 367. 1907 = *Prainea papuana* Becc.

ARTOCARPUS PONGA Dennst. Schlüssel Hort. Ind. Mal. 30. 1818, nomen illegitimum; Hassk. Hort. Mal. Rheed. Clav. 34. 1867 = *Hopea wightiana* Wall. ex Wight & Arn. Prodr. 85. 1834. This species is based on Rheede's *Ponga* (Hort. Ind. Malab. 4: 73. t. 35, 1683, as *Pongu* on the plate); I am indebted to the late A. H. G. Alston for its identification. Echininate galls bearing a superficial resemblance to the inflorescences of some species of *Artocarpus* frequently occur in *Hopea wightiana* and were shown in the illustrations of Wight (Ill. Ind. Bot. t. 37. 1840) and Beddome (Fl. Sylvat. t. 96. 1871). The appearance of these galls, and also of the leaves, agrees well with Rheede's picture, and the galls, which are formed from terminal or axillary buds, sometimes occur in clusters, as shown there. Rheede described these structures as calices containing several seeds, which were presumably the pupae of the insects. Brandis (Ind. Trees, 68. 1906) records *ila pongu* as a Tamil name for *Hopea wightiana*. No precise determination for *Ponga* appears to have been published previously, although the suggestion that it might be a species of *Broussonetia* was made by Hamilton in a key to the "Hortus Malabaricus" (Jour. Linn. Soc. 17: 195. 1835). *Artocarpus ponga* antedates *Hopea wightiana*, but this will not necessitate any nomenclatural change, since Dennstedt's name was based on a monstrosity (Int. Code, Art. 67. 1956).

ARTOCARPUS RIEDELI Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS SCANDENS Renner, Bot. Jahrb. 39: 367. 1907 = *Prainea scandens* King.

ARTOCARPUS TYLOPHYLLA Miq. Fl. Ind. Bat. 1(2): 289. 1859 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS VENENOSA Zoll. & Mor. Natur- en Geneesk. Arch. Ned.-Ind. 2: 213. 1845 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS VENENOSA Zoll. & Mor. var. TYLOPHYLLA Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89, 95. 1854 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS WOODII Merr. Philip. Jour. Sci. Bot. 3: 221. 1908 = *Parartocarpus venenosus* (Zoll. & Mor.) Becc.

ARTOCARPUS sp., Merr. Pl. Elmer. Born. 46. 1929 (*Elmer 20978*) = *Aporosa nitida* Merr. l.c. 143.

Two nomina nuda are also to be excluded from the genus.

ARTOCARPUS BIFARIA Wall. ex Miq. Ann. Mus. Lugd.-Bat. 3: 213. 1867, pro syn. *Sloetia sideroxylon* Teysm. & Binnend. ex Kurz, Jour. Linn. Soc. Bot. 8: 167. 1864, nomen superfluum = *Sloetia elongata* (Miq.) Koord. Exkursionsfl. Java 2: 90. 1912.

ARTOCARPUS ? ? FINLAYSONIANA Wall. Cat. no. 4662. 1831, nomen nudum = *Sloetia elongata* (Miq.) Koord. The two collections that were cited by Wallich under this number consist, in his herbarium at Kew, of specimens of *Sloetia elongata*. Wallich 4662A was collected by Finlayson and has abnormal, much branched inflorescences. Under the number 4662B there are two sheets collected from a plant in the Calcutta Botanic Garden which had been introduced from Penang. One bears a shoot with normal inflorescences. The other bears a single leaf and a label with the determination in Wallich's hand "*Morus* ? ? *bifaria* Wall." This suggests that the source of the name *Artocarpus bifaria* Wall. mentioned above is another sheet of this collection which had been assigned to the latter genus.

NOMINA DUBIA

ARTOCARPUS DIMORPHOPHYLLA Miq. var. MACROPHYLLA Miq. Fl. Ind. Bat. Suppl. 417. 1861. No specimens bearing this determination have been seen and the description is not identifiable.

ARTOCARPUS LAMELLOSA Blanco, Fl. Filip. 667. 1837, ed. 2. 465. 1847, ed. 3. 3: 74. 1880; Ahern, Timber Tree Sp. Philip. 35. 1901, excl. tab. The reasons for treating *A. lamellosa* as a *nomen dubium* are discussed above, under *A. nitidus* ssp. *nitidus*, which Merrill erroneously reduced to Blanco's species in 1905 (Publ. Gov. Lab. Manila 27: 80).

ARTOCARPUS PARVIFOLIA Voigt, Syll. Ratisb. 2: 53. 1828. The brief description of trilobed leaves, drawn up from a cultivated specimen from the garden of Belvedere, Thuringia, is not identifiable.

ARTOCARPUS RETICULATA Hunter ex Ridley, Jour. Str. Br. Asiat. Soc. 53: 114. 1909. Ridley thought that *A. reticulata* was probably referable to *A. lanceifolius*, and this seems likely, but the description is inadequate for identification.

ARTOCARPUS ROTUNDA (Houtt.) Panzer in Panzer & Christmann, Pflanzensyst. 10: 380. 1783; Merr. Jour. Arnold Arb. 19: 331. 1938. Merrill identified this plant with *Artocarpus rigidus* and it has been discussed under that species (Jour. Arnold Arb. 40: 153. 1959).

RADEMACHIA ROTUNDA Houtt. Nat. Hist. II. Pl. 11: 455. 1779. This is the basionym of *Artocarpus rotunda* (Houtt.) Panzer.

NOMINA NUDA ⁷

ARTOCARPUS ANGUSTIFOLIA Roxb. Hort. Beng. 66. 1814.

ARTOCARPUS BLUMEI Tréc. var. SARAWAKENSIS Boerl. Handl. Fl. Ned. Ind. 3: 370. 1900; Merr. Bibl. Enum. Born. Pl. 218. 1921.

ARTOCARPUS (?) FOENIFORMIS Eeden, Houtsoort. Ned. Oost.-Ind. 122. 1886, ed. 2. 242. 1905.

ARTOCARPUS MADAGASCARIENSIS Bojer, Hort. Maurit. 290. 1837.

⁷ The following list of names, published without description and of undetermined application, is appended for the sake of completeness.

ARTOCARPUS NEO-CALEDONICA Linden, Cat. 52. 1871; Guillaumin, Bull. Soc. Bot. Fr. 90: 35. 1943.

ARTOCARPUS OVATUS Noronha, Verh. Batavia. Genoot 5(5): 7. 1790. Noronha gives the Javanese name for this species as *riandelica* and this may be an error for *mandelica*, a name which is recorded for *Artocarpus rigidus*.

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SOME USEFUL TECHNIQUES IN THE STUDY AND INTERPRETATION OF POLLEN MORPHOLOGY

I. W. BAILEY

EACH OF THE VARIOUS TECHNIQUES that has been utilized in the study of pollen morphology has limitations as well as advantages. It is essential, therefore, that the conclusions attained by the use of any single technique be in harmony with those obtained by other techniques. This is particularly true where pollen is subjected to more or less drastic treatments during preparation for visual examination. In all such cases evidence should be obtained regarding the effects of each treatment upon the normal form and structure of living pollen.

A large amount of research in recent years has been focused upon the visible structure of the exine of acetylated pollen. Comparatively scant attention has been devoted to the study of the intine and the protoplast. If the various layers of the pollen wall are to be accurately defined and classified, it is necessary that more be learned concerning their chemical composition and physical properties. Summations of accumulated circumstantial evidence obtained by the use of diversified techniques can provide significant clues in this connection. In so doing, generalizations should be based, not solely upon the pollen of one or two randomly selected species, but upon investigations of a wide range of representative gymnosperms and angiosperms.

Mangin attempted to do this in a brief paper published in 1889. The significance of this paper cannot be adequately appreciated without reading Mangin's other papers dealing with the differential staining, differential solubilities, and other properties of the polysaccharides that occur in plant tissues in general. He recognized, not only that the intine differs markedly from the exine, but also that it is chemically heterogeneous. He concluded that it is composed of a mixture of polysaccharides, in most cases largely of cellulose and "pectose," the cellulose being concentrated adjacent to the protoplast and disappearing in the external zone or zones and particularly in the so-called "Zwischenkörper" of Fritzsche (1837) which commonly occurs in the apertural regions of the pollen wall. It should be noted in this connection that the results of Mangin's researches on pollen were published before he obtained a sample of ruthenium red (ammoniated oxychloride of ruthenium) from Joly (1892). He (1893) considered this dye superior, in the differential staining of pectic compounds, to such basic dyes as phenosafranin, methyl blue, etc., that he utilized so extensively in his earlier investigations. However, he does not appear to have used ruthenium red at a later date in an extensive investigation of pollen.

UTILITY AND RELIABILITY OF RUTHENIUM RED

In microscopy, ruthenium red has the advantage of being soluble in water but insoluble in alcohols, anhydrous glycerin, chloroform, benzene, xylol, clove oil, and other reagents utilized in preparing sections for microscopic examination. However, in aqueous solution it has the disadvantage of deteriorating rapidly in the light at ordinary room temperatures. This difficulty can be overcome by keeping solutions in the dark in a refrigerator. I have solutions of the dye (Edward Gurr, Ltd.) that are in good condition after more than a year. A more serious difficulty occurs in attempting to make permanent mounts of stained pollen, as also of sections of plant tissues. In all cases thus far the red color disappears in time from stained parts of the preparations.

There have been two extreme views regarding the utility of ruthenium red. At one extreme are those who assume that it is specific for pectic compounds, whereas at the other extreme are individuals who have shown that it stains a variety of chemical substances and therefore conclude that it is utterly "unreliable and useless in microchemical investigations. In this connection, I have made in the past extensive observations upon the staining reactions in aqueous ruthenium red of a wide range of inorganic and organic substances of known chemical composition. Tests have been made not only with naturally occurring gums and mucilages and pectic compounds and "polyuronide hemicelluloses" extracted from plant tissues, but also, through the cooperation of Professors Ernest Anderson and Karl P. Link, with fractions of these substances of known chemical composition. It seems that galacturonic and glucuronic acids when methylated, as salts, or in intimate chemical association with hexose and pentose sugars stain characteristically in aqueous ruthenium red. Where the substances themselves are soluble in water, their staining reactions may be studied by using a concentrated solution of the dye in admixture with a proportion of alcohol which inhibits or retards their rapid solution. In contrast to the general uniformity in the behavior of these naturally occurring substances, their free acids when isolated and purified are very variable in their reactions in aqueous solutions of ruthenium red. When they stain, they may give a yellow, rather than a red, coloration, and likewise may turn the color of the ruthenium solution from red to yellow. The rapidity and the intensity of staining varies in buffers of widely different pH. This raises complex questions regarding the effects of reagents in buffers upon the dye and upon the chemical composition of the substances being tested. Preliminary treatments of cells and tissues with acids, alkalies and other reagents should be avoided if possible. The most significant results are obtained when living cells or freshly cut sections of living tissues are quickly immersed in a solution of ruthenium red in distilled water or in relatively pure spring water.

Although the dye stains oxycellulose, hydrocellulose, the nucleus, protoplast, and other organic substances, as well as pectic compounds, gums, mucilages, and "polyuronide hemicelluloses," there are significant dif-

ferences in its behavior in these cases. In my investigations of cell walls of the higher plants, I have found that those naturally occurring polysaccharides which contain sugar acids (e.g., galacturonic, glucuronic) or their methylated or salt (e.g., calcium pectate) derivatives tend to stain very intensely and with extraordinary rapidity in dilute (1/5000) solutions of ruthenium red, whereas other naturally occurring organic substances, if they stain at all, do so more gradually and commonly less intensely. Of course, it should be realized in this connection that the staining may be inhibited or masked by lignification, cutinization, or suberization of cell walls. Thus, although the dye is not specific for pectic compounds and must be used with adequate precautions, its use does provide a simple and rapid method of obtaining useful clues or leads in studying the occurrence and distribution of polyuronides in plant cells and tissues. Although not conclusive by itself, it becomes increasingly so when in harmony with evidence obtained by other techniques, e.g., differential solubilities, polarized light, electron microscopy, etc.

The so-called intine of pollen commonly stains with remarkable clarity and rapidly when freshly collected pollen, viable dry pollen, dead pollen from herbarium specimens, and pollen preserved in alcohol are immersed in dilute aqueous solutions of ruthenium red. Frequently the differential staining is so rapid that it is clearly visible by the time that a mount can be made and examined under a microscope. In fact, it may sometimes be advantageous to retard the staining by using the aqueous solution in admixture with a high proportion of glycerin. Such admixtures are relatively stable when kept in the dark at ordinary refrigerator temperatures. Intense staining of the intine occurs first in the apertural region or regions of the pollen wall and subsequently in parts that subtend the exine. The exine does not stain, retaining its original greenish yellow or other colors. On the contrary the protoplast may in time develop a red coloration. The accelerated staining of thicker parts of the intine in apertural regions may be due to a higher concentration of stainable substances in such areas or to retarded penetration and diffusion of the dye through the exine of nonapertural parts. That the proportion of stainable substances varies is indicated by differences in the ultimate intensity of staining, not only as between the intines of different types of pollen, but also in different zones or layers of a single thick intine. That penetration of the dye is retarded or actually inhibited at times by the exine (or by external coatings of oily or resinous substances) is indicated by the fact that the intine of inaperturate pollen may not stain at times unless the exine is mechanically ruptured or abraded.

Ruthenium-red staining of the intine of pollen from herbarium specimens, as well as of freshly collected living pollen, provides a simple, rapid, and reliable means of studying variations in the normal form of the intine in the various taxa of the angiosperms. It is particularly useful in demonstrating variations in the form and thickness of the intine in apertural regions of pollen. Although the spectacular differences in color between the intine and exine require illustration in color, the intense red

staining of the thicker parts of the intine can be reproduced in intense black by the use of a green filter as illustrated in PLATE I.

The pollen of *Calycanthus* varies from monocolpate (Fig. 1) to zonaperturate or belted (Fig. 3) to bicolpate (Fig. 2) and infrequently to tricolpate. In each case the aperture or apertures are subtended by conspicuously thickened parts of the intine which stain intensely and with remarkable rapidity in dilute aqueous solutions of ruthenium red. In these pollen grains, as in those of *Illicium* (Fig. 4) which have three narrow grooves that extend from pole to pole,¹ the thicker parts of the intine are considerably broader than the transverse diameter of the furrows. This is in contrast to those forms of pollen (Fig. 5) in which the excessively thickened parts of the intine, "Zwischenkörper" of Fritzsche (1837), "oncus" of Hyde (1955), are but slightly broader than the diameter of the apertures. In the case of the Winteraceae, where the pollen occurs characteristically in tetrads, the New World representatives differ conspicuously from the Old World representatives of the family (Bailey and Nast, 1943). In the monoporate grains of the latter genera and species, the intine is somewhat thicker in the apertural part but does not protrude (Fig. 7), whereas in the New World representatives the protoplast protrudes and is jacketed by a thick coating of intensely staining intine (Fig. 8). In a majority of the angiosperms the thickenings of the intine subtend the apertures of varying form, size, and number, but this is not invariably the case, as has been shown by Dressler (1957) in the Euphorbiaceae. For example, in the tricolporate pollen of *Pedilanthus* (Fig. 6) there are six riblike thickenings which extend nearly from pole to pole. These thickenings of the intine are lateral to the elongated colpae, rather than directly beneath them.

OCCURRENCE AND DISTRIBUTION OF CELLULOSE IN POLLEN

Although the intense ruthenium-red staining of the outer part of the intine, particularly in apertural regions of pollen, is not necessarily indicative of pectic composition, it suggests, in correlation with the isotropy of this part in polarized light, plasticity during pollen tube emergence, expansion and contraction during wetting and drying, and solubility in cold 4% sodium hydroxide and other reagents which do not dissolve cellulose, that the outer part of the intine commonly contains a large proportion of uronide polysaccharides in its chemical composition.

As regards the inner part of the intine, the differing conclusions attained by Mühlethaler (1953) and Sitte (1953) by the use of electron microscopy raise an important question regarding the occurrence of cellulose in the inner part of the intine adjacent to the protoplast as hypothesized by Mangin (1893). In diversified representatives of both gymnosperms and angiosperms this part of the intine, although staining more or less

¹For illustrations compare Wodehouse (1935), page 336, Fig. 92, or Erdtman (1952), page 256, Fig. C.

intensely in ruthenium red, exhibits anisotropy in polarized light. Furthermore, it stains a characteristic blue when pollen grains are immersed directly in chloro-iodide of zinc or in 65% sulphuric acid following staining in iodine. Where the intine is very tenuous and obscured by the exine, the cellulosic part may be retained and rendered clearly visible by removing the protoplast and the noncellulosic constituents of the intine in 3% sodium hydroxide at 56° C. (Figs. 9-11).

Not only is the inner part of the intine insoluble in reagents which do not dissolve cellulose, but also it is removed by standard solvents of cellulose, e.g., 72% sulphuric acid, cuprammonium reagents, as well as during prolonged acetylation of pollen. Furthermore, its microfibrillar composition can be revealed by electron microscopy as demonstrated by Sitte (1953). In addition, it should be noted that when the noncellulosic constituents of the intine are completely removed the cellulose-containing inner layer no longer stains rapidly and intensely in ruthenium red.

In general (with the exception of certain unusual forms of pollen, e.g., *Eupomatia*), the cellulose-containing inner layer of the intine of both gymnosperms and angiosperms is tenuous and of relatively uniform thickness. This is in contrast to the striking variations in the thickness of the outer part of the intine that occur so frequently in various taxa of the higher plants. During the disruption of pollen walls due to differences in the contraction or expansion of the protoplast and wall layers, the cellulosic layer of the intine commonly tends to remain adjacent to the protoplast.

SOLUBILITY OF THE EXINE IN MONOETHANOLAMINE

The exine of pollen, like the cuticle of plants, is generally considered to be relatively inactive chemically since it persists for such prolonged periods in geological strata and dissolves only after prolonged drastic treatments. Much to my surprise, therefore, I have found that exines of freshly collected living pollen at anthesis (e.g., of such gymnosperms as *Taxus*, *Tsuga*, *Pseudotsuga*, *Pseudolarix*, and *Pinus* and of such angiosperms as *Liriodendron*, *Magnolia*, *Asimina*, *Taraxacum*, *Coreopsis*, *Ostrya*, *Populus*, and *Calycanthus*) dissolve in three hours or less when immersed in monoethanolamine at a temperature of 97° C. The only exceptions that I have encountered thus far in a preliminary investigation are pollen of *Ephedra* and *Pinus strobus* from old herbarium specimens and of *Eupomatia* preserved for a long period in F.A.A. fixative (formalin-acetic acid-alcohol). The fact that the exine of freshly collected pollen of *Pinus* dissolves suggests that changes occur under certain conditions of prolonged drying which inhibit solubility. Unfortunately no freshly collected pollen of *Ephedra* and *Eupomatia* is available, as yet, for such comparative purposes. In the case of *Liriodendron*, it is possible, by adequately controlling temperature and time of treatment, to remove the thick exine (Fig. 12) leaving the protoplast, the layers of the intine and oil globules but slightly modified visually (Fig. 13). Of course,

this raises an important question, viz., whether dissolving the exine of a large amount of pollen in monoethanolamine might yield a solute capable of separation and analysis. Such analyses might afford significant clues regarding the chemical composition of the exine and deserve to be more intensively investigated.

DISCUSSION

Summations of evidence obtainable by the application of diversified techniques indicate that the cellulosic part of the intine of both gymnosperms and angiosperms occurs in a comparatively narrow zone adjacent to the protoplast. The anisotropic cellulose occurs, however, in association with an isotropic polyuronide (or mixture of polyuronides and polysaccharides) which stains rapidly and intensely in dilute aqueous solutions of ruthenium red and which is readily removable by reagents which do not dissolve cellulose. The outer part of the intine, particularly in thickenings related to apertures, contains little, if any, cellulose and is composed of a polyuronide (or a mixture of polyuronides and polysaccharides) which stains and dissolves as does the material associated with the cellulose in the innermost part of the intine. The noncellulosic constituent in thicker parts of the intine (related to apertures in the exine) is plastic (i.e., easily penetrated or pushed aside during emergence of the pollen tube) and contracts and swells, with corresponding invagination and evagination, during drying and rewetting of living pollen. The consistency in the occurrence and behavior of this part of the intine in a wide range of taxa suggests that it serves two important functions, (1) to protect the protoplast in apertural parts of the wall and (2) to facilitate emergence of the pollen tube. Professor A. Orville Dahl and I plan to discuss this aspect of the intine in greater detail in a subsequent joint paper. We are also correlating evidence obtained by phase and electron microscopy and other diversified techniques in detailed studies of specific forms of pollen. The question of a revised terminology for wall layers, e.g., whether the use of intine should be restricted to the cellulosic layer and exintine or mesine used in referring to material that intervenes between the cellulosic layer and the exine, had best be deferred until comprehensive investigations of a wide range of representative pollen forms have been completed.

ACKNOWLEDGMENTS

This investigation was supported by a grant from the American Philosophical Society. I am much indebted to the curators of the Gray and Arnold herbaria for permission to collect pollen from a wide range of herbarium specimens, to Dr. A. C. Smith for assistance in obtaining pollen of the Winteraceae and other families, to Dr. C. E. Wood for pollen obtainable in his collection of flowers preserved in 70% alcohol, to Mr. L. J. Brass for collecting and preserving flowers of critical genera

in F.A.A. fixative, and to Dr. R. L. Dressler for living pollen of *Pedilanthus*. I am also indebted to Professors A. Orville Dahl and Kenneth V. Thimann for kindly reading the manuscript of this paper and for making a number of helpful suggestions.

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EXPLANATION OF PLATES

PLATE I

Pollen differentially stained in aqueous ruthenium red and photographed with a green filter at a magnification of 770. FIGS. 1-3, freshly collected living pollen; 5, 8, pollen from herbarium specimens; 4, pollen preserved in 70% alcohol; 7, pollen preserved in FAA fixative. FIGS. 1-3, *Calycanthus* sp. (cultivated, Cambridge, Mass.): 1, monocolpate grain viewed in optical section parallel to long axis of colpus; 2, dicolpate grain viewed in optical section parallel to the long axis of the colpus; 3, zonaperturate grain viewed in diagonal optical section. FIG. 4, *Illicium floridanum* Ellis (cultivated, Henry Foundation, Gladwyne, Pa.), tricolpate grain, polar view. FIG. 5, *Nouhuysia arfakensis* (Gibbs) Steenis (*Kostermans 2198* [A]), triporate grain. FIG. 6, *Pedilanthus* sp. (Dressler), tricolporate grain, polar view. FIG. 7, *Zygogynum Bailonii* Tiegh. (*Buchholz*, New Caledonia, 1947), each grain of the tetrad with a single more or less circular aperture. FIG. 8, *Drimys granadensis* L. f. var. *mexicana* (DC.) A. C. Smith (*Hinton 14441* [GH]), characteristic tetrad of New World section *Wintera*, each grain of the tetrad with a single aperture and protruding protoplast jacketed by a thick coating of stainable intine.

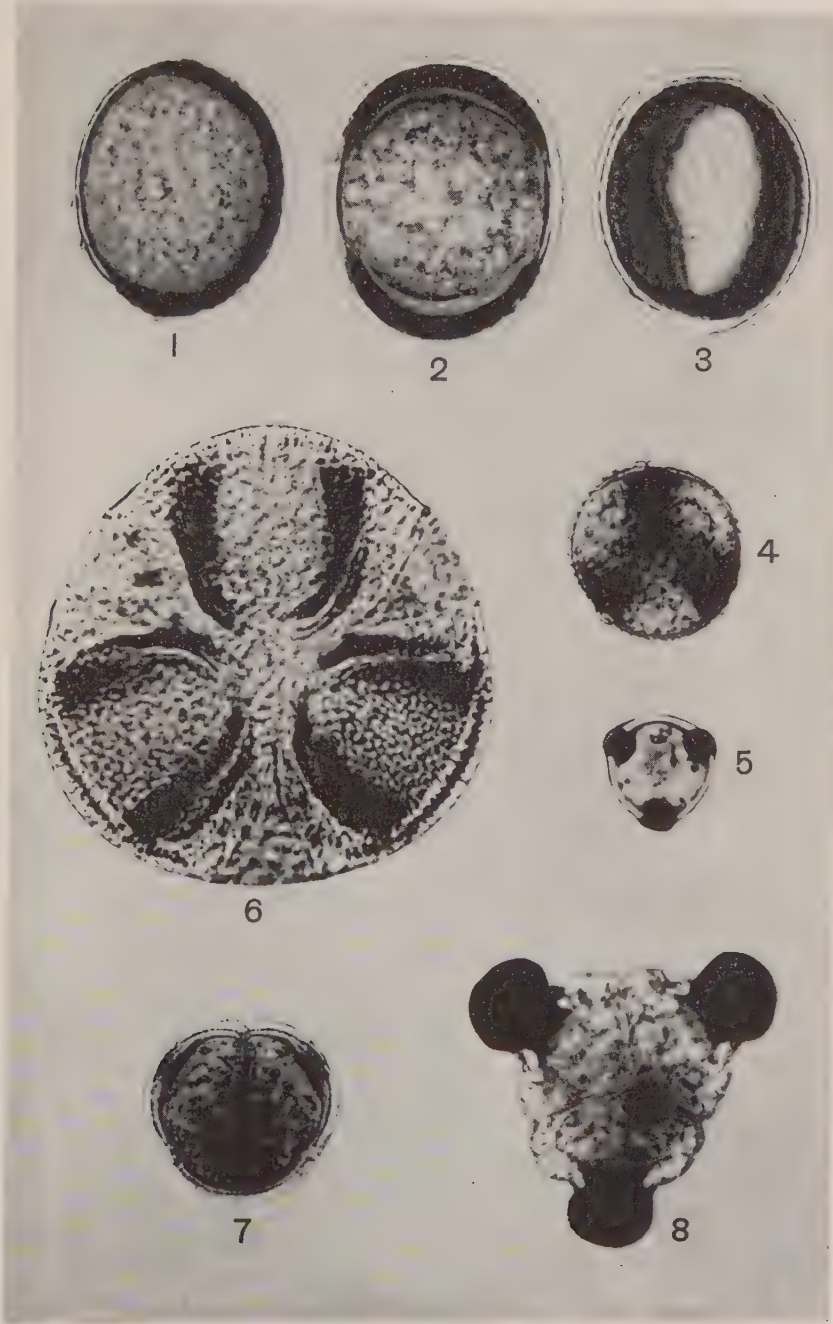
PLATE II

FIGS. 9, 10, *Liriodendron tulipifera* L. (cultivated, Arnold Arboretum): 9, pollen after treatment in 3% NaOH at a temperature of 56° C. which removes the protoplast and the noncellulosic constituents of the intine — when im-

mersed in chloro-iodide of zinc the contracted cellulosic residue of the intine stains a deep blue, in striking contrast to the greenish-yellow color of the exine, $\times 1130$; 10, characteristic anisotropy of two cellulosic residues in polarized light, $\times 400$. FIG. 11, *Pinus strobus* L. (Norwell, Massachusetts), freshly collected living pollen following the same treatment as in FIG. 9, $\times 1130$.

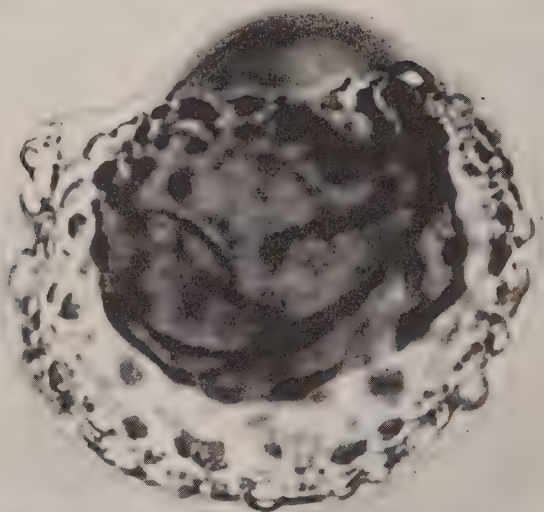
PLATE III

FIGS. 12, 13, *Liriodendron tulipifera* (cultivated, Arnold Arboretum): 12, freshly collected living pollen in a mixture of water and glycerine, viewed in optical section parallel to the long axis of the colpus, showing coarsely warty exine and conspicuous thickening of the intine in the apertural region, $\times 1130$; 13, pollen grain after a brief treatment in monoethanolamine at a temperature of 97° C.—exine has been removed leaving the intine, protoplast, and oil globules in place, $\times 1130$.

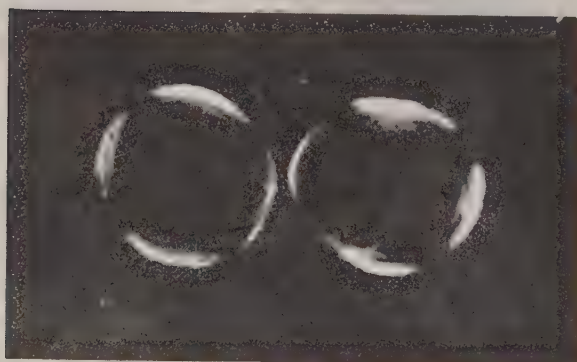


BAILEY, POLLEN MORPHOLOGY

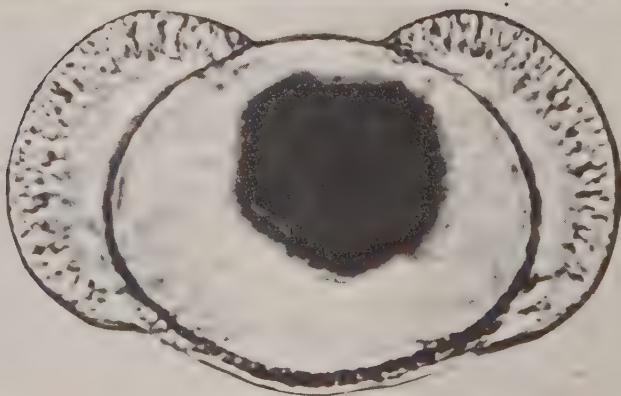
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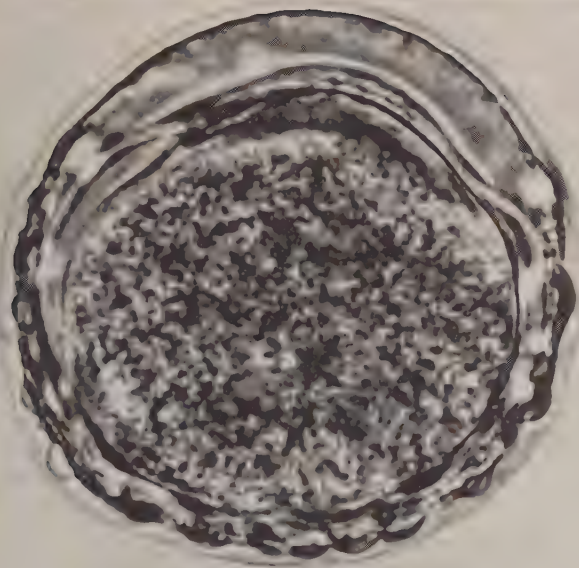


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11





12



13

THE GENERA OF SARRACENIACEAE AND DROSERACEAE
IN THE SOUTHEASTERN UNITED STATES¹

CARROLL E. WOOD, JR.

SARRACENIACEAE Dumortier (PITCHER-PLANT FAMILY)

Perennial, rhizomatous insectivorous herbs with tubiform or pitcher-like leaves. Flowers bisexual, solitary [or few and racemose], nodding, the scape naked [or few-bracteolate]. Flowers regular, 5[4,6]-merous, the insertion hypogynous. Sepals 5[4,6], free, imbricate at the base, persistent, sometimes colored [and petaloid]. Petals 5 [or none], free, deciduous. Stamens numerous, free, the filaments filiform, the anthers versatile, extrorse, 2-locular; pollen grains single, polycolporoidate to 5-6-colporoidate. Gynoecium syncarpous, the style simple below, the apex [entire or lobed or] peltate-dilate, the ovary 5[3]-locular, the placentation axile; ovules numerous, anatropous, 2-integumented. Fruit a 5[3]-valved, loculicidal capsule. Seeds numerous, small, winged [or not], with abundant endosperm, the embryo minute, near the hilum. TYPE GENUS: *Sarracenia* L.

A small, distinctive family of disjunct distribution, with three well-marked genera: *Sarracenia* (eight species of eastern North America), *Darlingtonia* Torr. (*D. californica* Torr. [*Chrysamphora californica* (Torr.) Greene], $2n = 30$, of northern California and southern Oregon), and *Heliamphora* Benth. (six species described from the isolated table-top mountains of northern South America).

The highly modified pitcher-leaves and the large, bisexual, pentamerous flowers with axile placentation are characteristic. The group has been allied with various families or combinations of families: Papaveraceae

¹Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. 39: 296-346. 1958). It may be remarked here, however, that the area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana, that descriptive material inapplicable to our species is included in brackets, and that references marked by an asterisk have not been checked. Other published portions of these studies will be found in Jour. Arnold Arb. 40, 41. 1959, 1960.

In connection with these families I am especially indebted for various comments and helpful suggestions to Dr. Patricia R. Roberts and to Dr. C. R. Bell, upon whose respective work on *Dionaea* and *Sarracenia* I have drawn heavily. I am also grateful to my immediate colleagues for their continuing interest and advice and to W. L. Brown, Jr., R. B. Channell, G. R. Cooley, D. Demaree, C. W. James, C. E. Jenner, J. Kucyniak, Jeanette Renshaw, H. F. L. Rock, and A. J. Sharp for their help in various ways. As in previous papers in this series, the illustration is by Dorothy H. Marsh.

and Nymphaeaceae or these plus Ranunculaceae; Droseraceae or Nepenthaceae, or both; Cephalotaceae; Francoaceae; Cistaceae. Although now placed with the insectivorous Nepenthaceae and Droseraceae by many authors, the true relationships are still in need of careful study in terms of the entire plant.

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1. *Sarracenia* Linnaeus, Sp. Pl. 1: 510. 1753; Gen. Pl. ed. 5. 226. 1754.

Perennial insectivorous herbs of bogs, seeping terraces and wet savannas. Plants rhizomatous, the 3–8 leaves clustered, erect and trumpet-shaped to decumbent and pitcher-shaped, liquid-filled to varying degrees, with a ridge or wing on the adaxial side and a terminally expanded hood; leaves green, yellow, maroon, or variegated; ensiform leaves sometimes present. Flowers solitary, nodding on erect scapes. Sepals 5, with 3 appressed, persistent bracts. Petals 5, yellow or maroon (or deep red), deciduous. Stamens 70–80 (arising in ontogeny in 10 groups). Gynoecium 5-carpellate; style simple below, the upper portion expanded into a large, persistent, 5-lobed umbrella-like structure, with a small stigma under each of the notched lobes; ovary 5-locular. Fruit 5-valved; seeds winged on one side. Chromosomes 2–4 microns long, similar, $2n = 26$. TYPE SPECIES: *S. purpurea* L. (Named for Michel Sarrazin de l'Étang, 1659–1734, physician at the Court of Quebec, who sent *S. purpurea* to Tournefort.) — PITCHER PLANTS, TRUMPETS, BUGLE-GRASS, BOG-BUGLES, DUMB-WATCHES, WATCHES, BUTTERCUPS, EVE'S CUPS, FROG-BONNETS.

Eight species, all confined to the southeastern United States, with the exception of *S. purpurea*, the most widespread species, which ranges from western North Carolina northward along the mountains and from southern Mississippi eastward and northward along the Coastal Plain to Newfoundland, Labrador, Mackenzie, and Saskatchewan.

Form and habit (and in some instances, color and marking) of pitchers

are the most useful taxonomic characteristics, in conjunction with color and shape of petals, odor, curvature of sepals, and presence of ensiform leaves. Leaf size is not a constant characteristic. (See Bell for key, ranges, and comments.)

The six species of sect. *ERECTAE* Uphof have upright, tubular or trumpet-shaped leaves with variously shaped hoods which largely prevent the entrance of rain. The group includes *Sarracenia leucophylla* Raf. (*S. Drummondii* Croom) and *S. rubra* Walt. with maroon petals, and *S. minor* Walt., *S. flava* L., *S. oreophila* Wherry, and *S. alata* (Wood) Wood (*S. Sledgei* Macfarl.) with yellow petals. The last three are closely related vicariads with yellow-green trumpet-shaped leaves bearing large hoods with more or less reflexed margins. They differ in ensiform leaves, hoods, petal shape and texture, and odor. Insofar as is known, the three are geographically separated: *S. flava* distributed on the Atlantic coastal plain (southeastern Virginia to western Florida and southern Alabama and a few disjunct stations inland in North Carolina); *S. oreophila* at the southern end of the Appalachians (northeastern Alabama to Elmore County, Alabama, westernmost central Georgia, and perhaps formerly Fentress County, Tennessee); and *S. alata* on the Gulf coastal plain (Mobile County, Alabama, to eastern Texas). *Sarracenia rubra* f. *Jonesii* (Wherry) Bell (*S. Jonesii* Wherry) has the fragrant maroon flowers, recurving sepals, and characteristically maroon-reticulate hoods of f. *rubra* and differs only in its larger leaves being more sharply expanded toward the leaf opening which is less closely covered than in f. *rubra*.

Sarracenia purpurea and *S. psittacina* Michx., both with maroon petals and decumbent pitchers and the latter with the most highly modified leaves in the genus, constitute sect. *SARRACENIA* (sect. *Decumbentes* Uphof). *Sarracenia purpurea* supposedly is represented southward by var. *venosa* (Raf.) Fern. (ssp. *venosa* (Raf.) Wherry), a doubtfully distinct taxon based upon proportions of "pitcher" and hood.

Sarracenia is confined to wet, mediacid soils and hence occurs largely in bogs, wet savannas, at the edges of pocosins, and on springy, sandy slopes on the Coastal Plain. The greatest concentration of species and individuals is in the southern half of Georgia and Alabama and in northern Florida. Only *S. minor* is known from peninsular Florida (as far south as Highlands County). The ranges of *S. purpurea*, *S. psittacina*, *S. leucophylla*, and *S. rubra* overlap at least in part those of all species except *S. oreophila*, which is completely isolated geographically.

The genus is a homoploid complex ($2n = 26$) of interfertile but morphologically distinct species. Sixteen of nineteen "geographically possible" natural hybrids have been reported from the wild, and two others have been produced artificially. Artificial hybrids involving three or four species have been made. No hybrids of *S. oreophila* are known. Most hybrids are sporadic where two or more species occur, but around Mobile Bay, where *S. leucophylla* and *S. alata* commingle, much hybridization and backcrossing are evident. The extent to which introgression occurs is not known. Over most of their ranges the various species seem to retain

their biological identities primarily through geographical and seasonal isolation.

The remarkable leaves are provided with nectar glands and are sometimes conspicuously colored (e.g., bright yellow-green to red in *S. flava*, the upper part of leaf and hood white, reticulate with red and green in *S. leucophylla*) or translucent spotted (*S. psittacina*, *S. minor*). Insects attracted by nectar or coloration may fall or crawl into the pitchers, and, if unable to escape, die and are digested. Only the pitchers of *S. purpurea* are water-filled; those of others which are provided with protective hoods secrete varying quantities of fluid, however. The morphological homologies of the leaves are still under discussion.

Sarracenias are fed upon by a number of moths known from no other plants: *Olethreutes* feeds upon the flowers and seeds; *Papaipema* is a rhizome-borer; and three species of *Exyra* eat the leaves. Other insects, including a sarcophagan fly, a gnat, a sciarid fly, and two harmless mosquitoes dwell in the pitchers. The larvae of the last, members of the tropical genus *Wyeomyia*, inhabit the water-filled leaves of *S. purpurea*. The larvae are purely aquatic and overwinter in the pitchers, surviving freezing and thawing. Pupation with subsequent emergence as the adult does not occur (at least in the North) until the proper photoperiod and suitable temperatures for growth are reached in the spring. Although pitcher-plants in some areas are accused of harboring mosquitoes, larvae of other genera do not occur in the pitchers, and the adult *Wyeomyia smithii* does not bite man.

Sarracenias are highly ornamental and were popular horticultural plants in Great Britain from about 1880 to 1890. With care, all of the species succeed in cultivation in pots filled with fine, sandy, acid muck and standing in about an inch of water. Full sunlight with a bright southeast-ern exposure is desirable. A cool, winter dormant period is usual.

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DROSERACEAE Salisbury (SUNDEW FAMILY)

Annual or perennial, rosulate or short-stemmed [or caulescent], insectivorous herbs of damp or wet soils [a few completely aquatic or of

dry soils], the leaves alternate, infolded or circinate in vernation, the blades modified as active traps (*Dionaea*, *Aldrovanda*) or equipped with mucilage-tipped irritable tentacles (*Drosera*, *Drosophyllum*). Roots mostly adventitious. Flowers bisexual, regular, the insertion hypogynous. Sepals and petals 5, free. Stamens 5–15 (–20), extrorse; pollen in tetrads (except *Drosophyllum*). Gynoecium syncarpous; styles 3[5] and deeply bifid [or otherwise divided] or single and with fimbriate stigma; ovary 1-locular with 3[5] parietal placentae or the ovules at the base of the locule; ovules anatropous, 2-integumented. Seeds small, numerous, the embryo minute, straight, embedded in abundant endosperm. (Including *Dionaeaceae* Small.) TYPE GENUS: *Drosera* L.

Four genera, *Drosophyllum* Link, *Dionaea* Ellis, *Aldrovanda* L., and *Drosera* L., the first three monotypic, *Dionaea* and *Drosera* in our area. The sensitive leaves, bisexual, usually pentamerous flowers, unilocular ovary, and parietal or basal placentation mark the family. Numerous reticulate interrelationships link all four genera and make separation into two families an arbitrary matter.

In addition to its present position, the family has been placed near the Violaceae and Ochnaceae in the Parietales (Violales) near the Saxifragaceae, and near the Lentibulariaceae. The validity of the present association with Sarraceniaceae and Nepenthaceae (the three constituting the Sarraceniales) is in need of careful examination, and the relationships of the family are still unsettled.

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KEY TO THE GENERA OF DROSERACEAE

- Leaf blades 2-lobed, hinged lengthwise in the middle, sensitive and closing, the marginal bristles interlocking; stamens mostly 15 (10–20); styles united; placentation basal. 1. *Dionaea*.
 Leaf blades linear to suborbicular, equipped on margins and upper surfaces with numerous gland-tipped irritable tentacles; stamens 5; styles 3, so deeply bifid as to appear to be 6; placentation parietal. . . . 2. *Drosera*.

1. *Dionaea* Ellis, Directions for bringing over seeds and plants from the East Indies and other distant countries, etc., 38. 1770; Nov. Act. Upsal. 1: 98. *pl.* 8. 1770.

Rosulate, scapose, insectivorous herbs, the leaf blades hinged medially and forming a sensitive trap, the petioles winged (scarcely so in full sun in summer), their bases forming a subterranean bulb-like structure around the short, horizontal, sympodial rhizome, the roots adventitious. Inflorescence from the terminal bud, cymose-umbelliform. Sepals 5. Petals 5, white, marcescent. Stamens usually about 15. Gynoecium of 5 united carpels, style 1, the stigma with numerous papillae, the ovary 1-locular, the placentation basal. Capsule opening irregularly; seeds obovoid, numerous, black and shining. Embryo sac development normal (*Polygonum* type). TYPE AND SOLE SPECIES: *D. Muscipula* Ellis. (Name from Greek, *Dione*, originally the mother of Aphrodite [Venus] but later used as "daughter of Dione," hence Aphrodite or Venus.) — VENUS' FLY-TRAP, FLY-TRAP.

Dionaea Muscipula ($2n = 30$ or $32?$) is known to occur only on the Atlantic coastal plain from Beaufort County, inland to Moore County,



Dionaea. D. Muscipula: a, habit, $\times 1/2$; b, mature leaf, $\times 1/2$; c, young leaf, the marginal bristles folded within the blade, $\times 1/2$; d, flower, $\times 1$; e, pollen tetrad, \times ca. 200; f, gynoecium, a portion of ovary wall removed to show basal placentation of ovules, semidiagrammatic, $\times 5$; g, open fruit, showing irregular dehiscence, seeds, and marcescent stamens and petals, $\times 2$; h, seed, $\times 10$; i, seedling (after Smith, 1931), $\times 8$.

North Carolina, and southward to the south bank of the Santee River, Charleston County, South Carolina. Roberts and Oosting suggest that the total range is determined by gross soil characteristics (those of the St. Johns soil series), while local populations are restricted by the depth to which the surface soil desiccates in dry periods and by light intensity. Fire influences the latter and helps to maintain the limited habitat which is ecotonal between wet, evergreen-shrub bogs (pocosins) and the dry sands of *Pinus australis-Aristida* savannas. The slow seed dispersal (probably by rain), the short period of seed viability, and the summer germination under rather particular requirements of high humidity and loose organic matter on a sand surface are additional factors.

Dionaea is famous for its bear-trap-like hinged leaf blades, each half of which is equipped with three sensitive bristles, which, when stimulated, cause the trap to close. Entrapped insects are prevented from leaving by overlapping marginal bristles and are digested by enzymes secreted by minute glands on the blade surface. Many problems remain in connection with the operation of the traps (which have been compared with those of *Aldrovanda*) and with the nutrition (both mineral and organic) of *Dionaea*. The occurrence of *Dionaea*, *Sarracenia*, *Drosera*, *Utricularia*, and *Pinguicula* together in soils low in mineral nutrients is suggestive.

Although often occurring in widely scattered colonies, the species is locally abundant. Vast numbers formerly were sold as novelties, only to perish in cultivation, but the plant is now protected by law in North Carolina (General Statutes of North Carolina, Section 14-129.1). *Dionaea* can be cultivated for scientific purposes in constantly moist peat or peaty sand in full sunlight with a cool, dormant period in winter. If grown in shade the petioles become more broadly winged, successive traps diminish in size and the plant eventually dies. (Bright light is also important in flower production.) Propagation may be by seeds or by cuttings from the vegetative parts or the inflorescence before the flowers open.

Flowering occurs from late May to mid-June (or July). Each proterandrous flower is open about three days. Seeds are shed by mid-July and germinate immediately. (Prompt storage under cold, moist conditions will maintain seed viability for up to a year, however.) Embryology and seed germination are similar to those of *Drosera rotundifolia*. In drying, leaves and flowers tend to blacken, as with various hemiparasites.

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2. *Drosera* Linnaeus, Sp. Pl. 1: 281. 1753; Gen. Pl. ed. 5. 136. 1754.

Perennial or annual, insectivorous herbs, mostly of acid sands and bogs; plants rosulate, scapose [or sometimes caulescent and up to 1 m. high]. Leaves usually petiolate, the blades suborbicular to filiform, the margins and upper surfaces in ours with irritable, gland-tipped tentacles; stipules present or absent. Flowers 5-merous, the petals white, pink, rose-purple [or yellow], marcescent. Stamens 5. Gynoecium of 3[5] united carpels, the 3 styles deeply bifid in ours, the ovary 1-locular with 3 parietal placentae. Capsule splitting between the placentae, 3-valved, with numerous minute seeds. Embryo sac development normal (Polygonum type). TYPE SPECIES: *D. rotundifolia* L. (Name from Greek, *droseros*, dewy, from the glittering, glutinous droplets secreted by the glandular tip of each tentacle.) — SUNDEW, CATCH-FLY.

More than 100 species in three subgenera, twelve sections, distributed primarily in the Southern Hemisphere (more than 50 species in Australia and New Zealand alone). Only sect. *DROSERA* (sect. *Rossolis* Planch.) is represented in North America. Seven well-marked species occur in

the United States, two, *D. linearis* Goldie and *D. longifolia* L. (*D. anglica* Huds.), entirely to the north of our area.

Characters of seeds, stipules and leaves are especially diagnostic in *Drosera*. The genus is vegetatively plastic in response to environment, and, as a result, seeds are among the most dependable taxonomic criteria. Petal color, seldom noted, varies in some species: the petals of *D. intermedia* Hayne, white or pinkish in the North, are purple in South America, and those of *D. brevifolia* Pursh, usually white or pink, are pink to purple in Texas (and perhaps in South America).

Drosera rotundifolia, of circumboreal distribution, extends southward on the Coastal Plain to southeastern Virginia (and Charleston, South Carolina?) and along the mountains to northern Georgia. Leaf shape, stipules, and pale sigmoid-fusiform seeds are characteristic. *Drosera capillaris* Poir. (*D. tenella* Willd.), vegetatively similar, but smaller, with ellipsoid seeds coarsely papillose-corrugated in 14–16 ridges, and with a very different range (Virginia to Florida and Texas; Cuba, Jamaica; northern South America; southern Mexico, British Honduras), is sometimes confused with this species. *Drosera brevifolia* (Virginia to Florida, Tennessee, Arkansas, Texas, Cuba, northern South America (?). Paraguay, Uruguay, and northern Argentina) lacks stipules and has glandular scapes and sepals and obovoid seeds with crateriform markings. *Drosera intermedia*, with conspicuous stipules, oblong-spatulate leaf blades, scapes which curve outward at the base, and oblong, densely papillate seeds, is of wide distribution from Europe to Newfoundland and westward to Minnesota, southward along the Coastal Plain to Florida and Texas, and to Cuba, Hispaniola, and northern South America. *Drosera filiformis* Raf. var. *filiformis*, with erect, filiform leaves to 25 cm. long, and purple tentacles and petals, is confined to the Coastal Plain from Cape Cod, Massachusetts, southward to southeastern North Carolina (? South Carolina and Georgia). Varietas *Tracyi* Diels (*D. Tracyi* Macfarl.), of western Florida and southern Georgia to Mississippi, seems to be separated geographically from var. *filiformis*, although it has been reported from South Carolina. It is a distinct taxon, differing in the larger leaves (to 40 cm. long), the greater size of the floral parts, and the green tentacles.

Section *DROSERA* is a polyploid group of about 40 species among which chromosome numbers of $2n = 20, 40$, and 80 are known. The North American taxa are diploid, with the exception of *D. longifolia* ($2n = 40$) which appears to be of amphiploid origin. (Species of other sections have been reported with $2n = 28, 32, 34$, and 60 .) Three naturally occurring diploid hybrids and two triploids, all sterile, are known from this section. Chromosomal sterility is indicated in one of the diploid hybrids. In some areas, *D. brevifolia*, *D. capillaris*, *D. filiformis*, and *D. intermedia* occur in close proximity, but hybrids are unreported in our area, although that of the latter two has been found once in New Jersey. An artificial hybrid might show whether a genetic barrier exists between *D. filiformis* var. *filiformis* and var. *Tracyi*.

The leaves of *Drosera* catch and digest various small animals (mostly

insects) which become entangled in the mucilaginous secretion of the tentacular glands. The tentacles bend inward, pressing the capture against the leaf blade which, in some species (e.g., *D. rotundifolia*, *D. intermedia*, but not *D. filiformis*), may also bend enfolding the prey. Both movements involve cell elongation; a single tentacle is capable of bending approximately three times before the limit of growth is reached.

The genus exhibits remarkable regenerative powers, and, in some species (e.g., *D. rotundifolia*), asexual reproduction by adventitious plantlets from inflorescences or detached leaves is common. Individual flowers of the scorpioid (rarely forked) cyme are open for only a single morning in sunlight and are self-pollinated upon closing if cross-pollination has not already occurred. Some of our species produce overwintering buds of tightly compacted leaves, but *D. brevifolia* apparently behaves as an annual in many areas and has been so described (*D. annua* Reed).

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A REVISION OF THE GENUS *CLETHRA* IN CHINA

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TWENTY SPECIES OF *CLETHRA* have been recorded from China. Ninety per cent of these were described as new entities. These descriptions were prepared by British, French, American, Austrian, Dutch, and Chinese botanists, and their research was conducted in nine different European and American botanical institutions. In reviewing their work, it becomes apparent that some of them had no proper understanding of the variability of a species of *Clethra*. Consequently, repetition and confusion were created for the taxonomy of the Chinese species. Under these conditions the naming of a new collection of *Clethra* becomes a seemingly hopeless task. Even in the herbarium of the Arnold Arboretum where outstanding collections of Chinese specimens, including many types and photographs of types accompanied by fragments of the type-material, are deposited, one found it difficult to name an unidentified specimen of *Clethra*. A generalized treatment of the genus which contains a well-balanced key to the species and concise descriptions of them to aid in the identification of specimens is lacking. To supply such a treatise is the immediate aim of this revision.

The genus *Clethra* has an Asiatic-American distribution. An analysis of the countries of origin of the species as listed in the *Index Kewensis* shows that China and Mexico have the largest numbers of species. Careful examination of the species described from these two countries and their adjacent land-masses indicates that morphological variations among the Chinese species are far more diverse than among their tropical American allies. Actually, all the outstanding morphological features of the American species can be found among some of the Chinese species; yet the variations of certain Chinese forms are not to be found among the New World species. For this reason, a systematic revision of the Chinese *Clethra* has a more far-reaching significance than the merely utilitarian aim mentioned above. It seems that the problems involved in the classification of Chinese *Clethra* constitute the core of investigations which may lead to an understanding of the morphology, taxonomy, and geographical distribution of the genus as a whole. A proper knowledge of the Chinese species may throw some light on future studies of the American species.

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Unless accompanied by a note of explanation, all the specimens cited in this article are deposited in the herbaria of the Arnold Arboretum and the Gray Herbarium.

HISTORY

The genus *Clethra* was established on a North American species, *C. alnifolia*, originally known to European naturalists from Carolina and Virginia. The name *Clethra* (derived from the ancient Greek name for the alder, *klethra*, in allusion to the resemblance of the leaves of the type species to those of *Alnus*) first appeared in Gronovius' *Flora Virginica*, published in 1739. When Gronovius created this name he cited two earlier references, one from Plukenet's *Phytographia*, published in 1691, and the other from Catesby's *The Natural History of Carolina*, published from 1731 to 1743. He even quoted Catesby's diagnostic comment on the taxon intact, "Alni folia Americana serrata, floribus pentapetalis albis, in spicam dispositis." Linnaeus used Gronovius' name, giving the same quotation. A specimen of *C. alnifolia* is preserved in the Linnaeum herbarium, number 567.1. The species was introduced into European gardens in the early eighteenth century.

For a century and a quarter after the establishment of the genus, the classification of *Clethra* was based principally on American species. In 1839, De Candolle, in his *Prodromus*, placed *Clethra* in the tribe Andromedae of the family Ericaceae. His description of the anthers represented an erroneous observation. Apparently he mistook the developmental stage in the flower bud to be the mature anther and, though he did mention the inversion, he interpreted the cordate portion as the base and the mucronate and muticous end as the apex. In regard to the classification of the species, he arranged those known at that time in two sections, *Euclethra* and *Cuellaria*. He characterized his section *Euclethra* as having exserted stamens and pistils and deciduous leaves, and placed five North American species in this section. He characterized the section *Cuellaria* as having the stamens and pistils included and assigned 17 species from Central and South America and a single species from the Madeira Islands to this section. Although Blume had published *C. canescens* Reinw. from Celebes and Borneo, De Candolle did not include this species in his system.

In 1851 in an article, *Studien über die natürliche Klasse Bicornes*, Klotzsch separated *Clethra* from the family Ericaceae and raised it to a family, Clethraceae, on the strength of its choripetalous corolla, corolla and stamens deciduous after anthesis, its obcordate anthers which are retroflexed at first and then introrse and dehiscent by apical rimiform pores, and its bifid or trifid stigmas.

The portion of the Bentham and Hooker's *Genera Plantarum* that covers *Clethra* was prepared by Hooker. In this work Hooker placed *Clethra* at the end of the family Ericaceae as "Genus Anomalum." By this time several species had been introduced into cultivation in England, e.g., *C. arborea* from the Madeira Islands, *C. quercifolia* from Jalapa in Mexico, *C. tomentosa* and *C. alnifolia* from eastern North America. With live plants as well as herbarium specimens at his disposal, he gave the most accurate description of the important characters of the genus. Re-

garding the anthers, he pointed out that they are affixed at the middle of the back, are often obovate in shape and acute at the base, are extrorse at first then turning introrse, and dehisce above the middle by elongate pores.

The Chinese *Clethra* were not known to botanists until 1883. In that year Hance published *C. faberi* from Loh-fau Mountain of Kwangtung Province. Two years before this, Franchet, in his *Plantae Davidianae*, had published *Clethra scandens*. However, this species is not a true *Clethra*, and since then has been made the type species of the genus *Clematoclethra* Maxim.

When Hemsley prepared the enumeration of the plants from China, he saw Henry's collections of *Clethra* from Hupei. He was indeed not critical in his observation. In publishing Forbes and Hemsley's *Index florum sinensis* in 1889, he treated Henry's collections as *C. canescens* Reinw., a species known only from Western Malaysia. In the same work he reduced *C. faberi* Hance (from Kwangtung), *C. lancifolia* Turcz. (from the Philippines), and *C. barbinervis* Sieb. & Zucc. (from Japan) to *C. canescens*.

In the same year O. Drude published his contributions on Clethraceae, Ericaceae, and other related families in Engler and Prantl's *Die natürlichen Pflanzenfamilien*. In this work Drude accepted Klotzsch's proposal of raising the genus to a family and in the description of the genus, followed Hooker. In the classification of the species, he adopted De Candolle's two sections and placed the Asiatic species *C. barbinervis* in section *Eucléthra*. He separated *C. arborea* Ait., a species from the Madeira Islands, from section *Cuellaria* and assigned it to an unnamed section which he placed between *Eucléthra* and *Cuellaria*.

Meanwhile, material collected by French missionaries who were stationed in central and western China reached Paris. Franchet in 1895 published *C. fargesii* from eastern Szechuan and *C. delavayi* from western Yunnan. Incidentally, these species define the northern and western limits of the range of the genus in China.

Bodinier, Cavalerie and Esquirol were French missionaries who were sent to Kweichow in later years. Their collections reached Lévêillé who in 1912-3 published six more species of *Clethra*: *C. bodinieri*, *C. cavaleriei*, *C. esquirolii*, *C. kaipoensis*, *C. lineata* and *C. pinfaensis*. As indicated by a key to these species which he prepared in the *Flore du Kouy-Tchéou*, Lévêillé observed several characters which are important for distinguishing the Chinese species of *Clethra*. He observed that some species possess entire stigmas, while others have lobate or cleft ones. He also noticed that some species have elongate pedicels, while others have short ones. The arrangement of the racemes was also mentioned in his key, as some were umbellate while others were solitary.

After E. H. Wilson returned from his third trip to West China, Rehder and Wilson worked cooperatively on Wilson's numerous collections. In 1913, they described *C. monostachya*, a species characterized by its pilose styles. When Rehder worked over the ligneous plants described by Lé-

veillé, he was able to examine the types of Lévillé's six species of *Clethra* which were described from Kweichow. In 1934 Rehder recognized three of them and merged *C. esquirolii* and *C. lineata* with *C. cavaleriei* and *C. pinfaensis* with *C. kaipoensis*.

Aside from the species described by these workers, seven additional binomials were added to the genus by Handel-Mazzetti, Sleumer, Hao, Fang, and Li. None of these authors seems to have attempted to place his species in the existing taxonomic system, and some of these names are synonymous with earlier described species.

TAXONOMIC CHARACTERS

Habit of growth. The species of *Clethra* generally have the habit of growth common in the family Ericaceae. The branches have subverticillate branchlets with leaves crowded at the apex. The majority of the Chinese species are deciduous and two of them are evidently evergreen.

In the deciduous species, each vegetative branchlet has a large, sessile terminal bud and 1-3 subterminal axillary buds (FIG. 24, right). In the following year, the large terminal bud of a mature plant develops into a flowering shoot provided with a few smaller leaves, a bracteate raceme or panicle, and 1-3 axillary buds immediately below the inflorescence (FIG. 24, left). The subterminal buds of a vegetative branchlet and the axillary buds of a flowering branchlet are of the same nature and function. They are all active during the growing season and consequently attain various stages of development before the leaves fall in the autumn. The more vigorously growing ones develop into stems 4-6 cm. long, each bearing 3 or 4 leaves crowded at the shoot apex around the terminal winter bud. The weaker ones generally develop into short stems 1-2 cm. long, each bearing 1 or 2 very small, bract-like leaves surrounding the terminal winter bud. Often the stem-portion becomes so short that the bud appears as though it were a stalked winter bud. In this case, it bears no leaf. In the next growing season these winter buds either unfold and develop into short vegetative shoots with large leaves and strong, fat terminal buds ready to produce flowers the third year, or they may develop into flowering shoots, depending upon the vigor of the plant, the environmental condition, and the heredity of the species.

In an evergreen species, an average branchlet of a mature plant is usually a flowering branchlet (FIG. 25). From one to four axillary buds immediately below the inflorescence develop into leafy shoots, each bearing a terminal bud and several normal leaves crowded at the apex. Normally, this terminal bud produces a flowering shoot during the next growing season. The inflorescences of the Chinese evergreen species are all simple racemes.

Schneider in 1910 observed the evergreen habit of *C. arborea* Ait. and used it as a key character in the classification of the then-known cultivated species of *Clethra*. With the Chinese species the evergreen habit

is correlated with an entire stigma. It is an obvious key character for distinguishing species.

Leaves. The leaves on the branchlets of a deciduous species are of two kinds. Those developed from a winter bud are the normal leaves and are usually the larger ones. Those developed from axillary buds which become active during the same season in which they are produced are always smaller and narrower. They often become bract-like and are more pubescent than the normal leaves on the same plant. In the study of *Clethra*, whenever the comparison of leaf-characters is employed, care must be exercised so that the comparison is made between leaves of the same origin. With the Chinese species, the normal leaves of a species seem to be quite stable in shape, indumentum, dentation and venation. Any variation occurring in these respects is usually correlated with some flower character, and, for this reason, the leaf-characters are used as auxiliary criteria for distinguishing species.

Inflorescences. The Chinese species of *Clethra* are summer bloomers. The earliest flowering species, *C. bodinieri*, begins to flower in June and its fruits mature in early August. The latest flowering species, *C. kaipoensis*, is in full bloom in middle September. The majority flower in July and August, however.

The inflorescences of most Chinese species of *Clethra* are either simple terminal racemes (FIGS. 25, 26), or paniculate racemes. The panicles are sessile and subumbelliform (FIG. 27). The inflorescences of weak or old branchlets of a species normally bearing panicles may appear simply racemose. However, a good specimen of the species usually has paniculate inflorescences. The form of inflorescences, when correlated with leaf and flower characters, is a convenient and rather reliable character for distinguishing species. For this reason, it has been used as a key character in most manuals.

Rachis. The rachises of all the species of *Clethra* are densely pubescent. Those of the majority of the Chinese species have stellate hairs, but the rachises of *C. bodinieri* have simple, straight, appressed hairs. The type and density of the indumentum on the rachises is a useful aid in the recognition of species.

Bracts. The bracts subtending individual flowers have been used by American botanists for distinguishing *C. alnifolia* and *C. acuminata*. Some botanists put special emphasis upon the relative length of the bracts and the flowers. Actually, the bract is a rather poor character to employ for distinguishing species, for the bracts of *Clethra* are caducous. In general, the first opened flower of a raceme is situated a little below the middle of the inflorescence and the other buds open progressively towards both ends. The bracts and the mature flowers are not present at the same time (FIGS. 26, 27). It is only when the inflorescences are in the bud stage that the flower buds are subtended by bracts. The degree

of maturity of the inflorescence makes a great difference in the relative length of the bracts and the flowers. This character should be used with great caution. It can never be used as the only criterion for distinguishing species.

Pedicels. The pedicels of *Clethra* exhibit a definite pattern of elongation during anthesis. As illustrated by FIGS. 1-6, which show stages from a fully grown flower bud to the dropping of the petals, the pedicels normally increase three times in length. The lengths of the pedicels of individual flowers of a species at comparable stages of development are rather uniform, however, and, for this reason, the Chinese species may be divided into two distinct groups, the long-pedicellate and the short-pedicellate.

Species in the long-pedicellate group have pedicels 5 mm. or more long immediately before anthesis (FIG. 1). When the petals begin to open, the length of the pedicels has doubled (FIG. 2), and by the time the petals drop off, the pedicel is three times as long as that of a mature flower bud (FIG. 3). After anthesis the pedicel elongates slightly; therefore the fruiting pedicel of a species is longer than that of the flower.

The pedicels of the short-pedicellate species are 1-2 mm. long immediately before anthesis (FIG. 4) and are normally shorter than the sepals. During anthesis, these pedicels elongate three-fold. As the sepals do not increase in size during this period, the length of the pedicels and that of the sepals are almost equal (FIGS. 5, 6).

The relative length of the pedicels and sepals is a reliable taxonomic character in *Clethra*. In employing this character one may use it only when the pedicels of the specimens are in comparable stages of development.

Calyx. The Chinese species of *Clethra* are distinctly gamosepalous. The calyx is essentially patelliform, deeply divided into 5 lobes. The short united portion is truncate and ridged at the basal end. The imbricate lobes vary in shape and size. The calyx attains mature size early in the development of the flower and maintains its shape and size during anthesis. Thus the calyx of a young flower bud and that of the young fruit of a species are about the same shape and size.

The calyces of the Chinese species of *Clethra* differ in the degree of division and in the shape and size of the lobes. The calyx of *C. bodinieri* is cut half way to the middle and its lobes are ovate, only 3 mm. long (FIG. 7). The calyx of *C. delavayi* is deeply cut with lanceolate lobes (FIG. 9) while the calyx of *C. kaipoensis* is deeply cut with oblong lobes (FIG. 8). The characters drawn from the calyx and sepals are reliable and are usually correlated with the length of the pedicel, the shape of the petals, and the relative length of the filaments. They can serve as good criteria for distinguishing sections and series.

Corolla. All the species of *Clethra* are choripetalous. Like the sepals, the petals of different Chinese species of *Clethra* can be grouped into three types. In *C. bodinieri* the petals are oblong, ciliate along the margin, ven-



FIGS. 1-23. MORPHOLOGICAL DETAILS OF CHINESE SPECIES OF *CLETHRA*.

FIGS. 1-6. Elongation of pedicels during anthesis, showing stages before, at, and after anthesis, $\times 1$: 1-3, a long-pedicellate species, *C. esquirolii* (Tsoong 83440); 4-6, a short-pedicellate species, *C. brammeriana* (Wang 247).

FIGS. 7-9. Calyces, $\times 3$: 7, shallowly divided calyx of *C. bodinieri* var. *parvifolia* (Tsang 22450) with ovate lobes; 8, deeply divided calyx of *C. delavayi* (Delavay 3319); 9, deeply divided calyx of *C. kaipoensis* (Tsang 27916) with oblong lobes.

FIGS. 10-12. Stamens, $\times 7$: 10, *C. cavaleriei* (Tsang 21413), stamen from rather large flower with exserted stamens—note glabrous filaments, V-shaped elongate anther, slim thecae, elongate rimiform apical pores, and long basal process; 11, *C. delavayi* (Forrest 11590), stamen from large flower with included stamens—note villous filament, oblong-obovate anther, rather plump thecae, broad apical pores, short basal process; 12, *C. brammeriana* (Wang 247), stamen from small flower with exserted stamens—note glabrous filament

trally barbate, and emarginate at the apex (FIG. 7). In *C. delavayi* the petals are large, almost entire, neither ciliate nor barbate, and are longer than the stamens (FIG. 8). In *C. faberi* and *C. kaipoensis* the petals are obovate, fringed, glabrous or slightly villose on the inside, and shorter than the stamens (FIG. 9). Petal characters, when correlated with characters of the pedicel, sepal, and stamen, can be used for distinguishing series.

Stamens. A flower of *Clethra* has ten stamens disposed in two whorls, the outer opposite the petals, and with shorter filaments (FIG. 13). In *C. bodinieri* the sepals and anthers are slightly longer. In *C. barbinervis* the difference in the size of the anthers is not appreciable.

The filaments of *Clethra* may be glabrous, hirsute, or villose. The indumentum of the filament has been used as a specific character. Before experimental evidence of the importance of hairs in the speciation of *Clethra* is available, this easily detected character is used for distinguishing species.

In the historical review we have noted that Hooker in 1876 gave a very accurate description of the stamens of *Clethra*. He pointed out that the anthers of this genus are obovate and the thecae dehisce above the middle by elongate pores. It appears now that in some widely accepted manuals and text books on the taxonomy of vascular plants published in recent years, different descriptions of the anthers and their dehiscence are given. Some of these statements give a rather incomplete picture, while others involve inaccurate observations. For example, Fernald in 1950 stated, "anthers extrorse in bud and opening by pores at base and inverted in flower" and Lawrence in 1951 noted, "anthers 2-celled, extrorse, sagittate, inverted and inflexed in bud, dehiscing by apical pores." The determination of the apex and base of an anther and the introrse or extrorse dehiscence of its thecae depends upon the attachment of the anther to the filament. The anther in *Clethra* is dorsifixed, often appearing versatile at

abruptly enlarged at base, very short obcordate anther, rather plump thecae, small apical pores.

FIGS. 13-16. Stages in maturation of stamens to show straightening of filaments in *C. cavaleriei* (H. H. Chung 2932), $\times 5$: 13, position of young anthers in half-grown bud, sepals and petals removed, anthers in an upside-down position, outer whorl of stamens with short filaments; 14, adaxial view of young stamen and petal, showing bend of filament below point of attachment; 15, same, at a later stage of development, showing knee-shaped bend produced by elongation of filament; 16, lateral view of stamen and petal at a more advanced stage, the filament almost straightened.

FIG. 17. Fully opened flower of *C. bodinieri* (Tsang 22450), showing short stamens of outer whorl and long stamens of inner whorl, some petals and stamens removed, $\times 5$.

FIGS. 18-20. Pollen grains of *C. delavayi*, *C. bodinieri*, and *C. faberi* respectively.

FIGS. 21-23. Style and stigma types, $\times 10$: 21, trifid style with three stigmas (*C. cavaleriei*); 22, undivided style with 3 apical lobes, 3 stigmas (*C. brammeriana*); 23, undivided style with single punctiform stigma (*C. bodinieri*).



FIGS. 24-27. Habit and inflorescence types of Chinese species of *Clethra*, $\times \frac{1}{2}$. 24, Flowering branchlets of *C. esquirolii* (Steward & Cheo 394), showing formation of vegetative shoots from active axillary buds; 25, Fruiting branchlet of *C. bodinieri* var. *parvifolia* (Tsang 23822), showing leaves on growth of two years; 26, *C. delavayi* (leaf, Delavay 3319; flowering branchlet, Forrest

anthesis. A mature anther is V-shaped (FIG. 10), obovate-oblong (FIG. 11), or obcordate (FIG. 12). The thecae dehisce by rimiform apical pores situated slightly on the ventral side of the anther.

In a flower bud, the inverted position of the anther is caused by the outward folding of the filament which occurs at a point about one-fifth below the attachment of the anther (FIGS. 13, 14). As the flower opens, the apical half of the filament increases in length several times faster than the basal half becoming geniculate in character (FIG. 15). The tension created by the elongating filament pushes the anther up (FIG. 16) and as the filament becomes straightened, the anther is set at its normal position with the apical pores pointing upward and inward (FIGS. 1-12, 17). In 1952 Kavaljian published on the floral morphology of *Clethra*, and regarding the inversion of the anther he stated, "the morphological base becomes the apparent apex." This statement is unnecessary because the rolling and folding of filaments in flower buds and the straightening of the filaments at anthesis are as common as the veneration and the unfolding of leaves. They are normal processes of growth. In *Clethra* the change of position of the anthers from bud to fully grown flower occurs in the filaments, not at the points of attachment of the anthers to the filaments. Therefore, what Kavaljian termed the "apparent apices" of the anthers are the "morphological apices."

Because of the change of the length of the filament during the short period of anthesis, specimens collected at different stages in the development of the flower may have different appearances. For this reason the nature of the flower in regard to its included or exerted anthers is not a very satisfactory criterion for distinguishing species. It can be used only as an auxiliary character. Variations in the size and shape of the anthers of different species are obvious. The longest anthers, such as those found in *C. bodinieri* and *C. cavaleriei*, are 2.5-3 mm. long, V-shaped in outline, deeply parted above, with relatively slim thecae and elongated rimiform apical pores (FIG. 10). The medium-sized anthers, such as those found in *C. delavayi* and *C. monostachya*, are 1.75-2 mm. long, obovate-oblong in outline, moderately parted above, with rather plump thecae and short and wide apical pores (FIG. 11). The short anthers, such as those found in *C. kaipoensis* and *C. brammeriana*, are only 1 mm. long, obcordate in outline, shallowly parted above, the thecae short, plump and with small apical pores (FIG. 12). Anther characters correlate with the size of flowers and the shape and sizes of sepals and petals. They can be used as auxiliary characters for distinguishing sections or series.

Pollen grains of *C. delavayi*, *C. bodinieri* and *C. faberi* taken from herbarium specimens were examined. They differ in shape and structure in their apertures (FIGS. 18-20). The grains of *C. delavayi* and *C. faberi* are tricolporate. The grains of *C. faberi* lack the protruding roof of the ora which Erdtman considered to be a characteristic feature of the pol-

15889); 27, *C. fargesii* (Henry 7270), showing subumbelliform racemes, small vegetative shoots developed from active axillary buds.

len of the genus. The pollen of *C. bodinieri* seems to be porate and not colporate. The significance of pollen morphology in the taxonomy of infrageneric groups of *Clethra* awaits further research and judgment by competent palynologists.

Pistil. The pistil is tricarpellate. The ovary is always pubescent, while the style may be pubescent or glabrous, trifid or undivided at the apex. The presence or absence of hairs on the style has been used as a specific character, and this practice is adopted here. The trifid style has three terminal stigmas (FIG. 21). Most of the Chinese species of *Clethra* have trifid styles. The undivided style may have 3-lobed stigmas such as are found in *C. brammeriana* (FIG. 22), or it may have a single punctiform stigma such as is found in *C. bodinieri* (FIG. 23). The type of style and stigma may be used as an auxiliary character for distinguishing species in *Clethra*.

Fruits. The fruit is a loculicidal capsule with persistent sepals and style. The relative length of the fruiting pedicels is a helpful character for distinguishing species. There seems to be a positive correlation between the size of the flower and fruit of a species. The fruits of the large-flowered species *C. delavayi* are 4–6 mm. in diameter, while those of the small-flowered species *C. kaipoensis* are 2.5–3 mm. in diameter. Most of the herbarium specimens which I have examined lack fruits, and their significance in the classification of the species is not emphasized.

Seeds. Material with fully grown seeds is scarce in our herbaria. The seeds of *C. bodinieri*, *C. barbinervis*, *C. cavaleriei*, *C. delavayi* and *C. monostachya* were examined. Those of the first three species are irregularly angular, extremely reticulate and not winged. The seeds of *C. delavayi* and *C. monostachya* are slightly compressed, 1 mm. long, 0.5 mm. wide, reticulate and the cells along the margin are enlarged, but no wings are evident. The seeds of the Chinese *Clethra* are very different from the highly compressed and winged seeds of the North American species.

ECOLOGICAL NOTES AND GEOGRAPHICAL DISTRIBUTION

The Chinese species of *Clethra* are essentially mountainous forms. They occur in thickets or at the margin of woods in acid soil. The available material in our herbaria indicates that there are two distinct groups of species, the western and the eastern, which are separated by six hundred miles. No collection of *Clethra* has been recorded in the area in between.

The western species constitute a small series, *Delavayanae*, of high mountain forms. They usually occur at altitudes of 2400–3800 meters. *Clethra delavayi*, *C. yuiana*, and *C. monostachya* belong to this group. In *C. delavayi* a glabrous variety has been recorded from a higher altitude than the pubescent variety. In this western range, *C. monostachya* occurs in the North and *C. delavayi* and *C. yuiana* in the South (MAP 1).

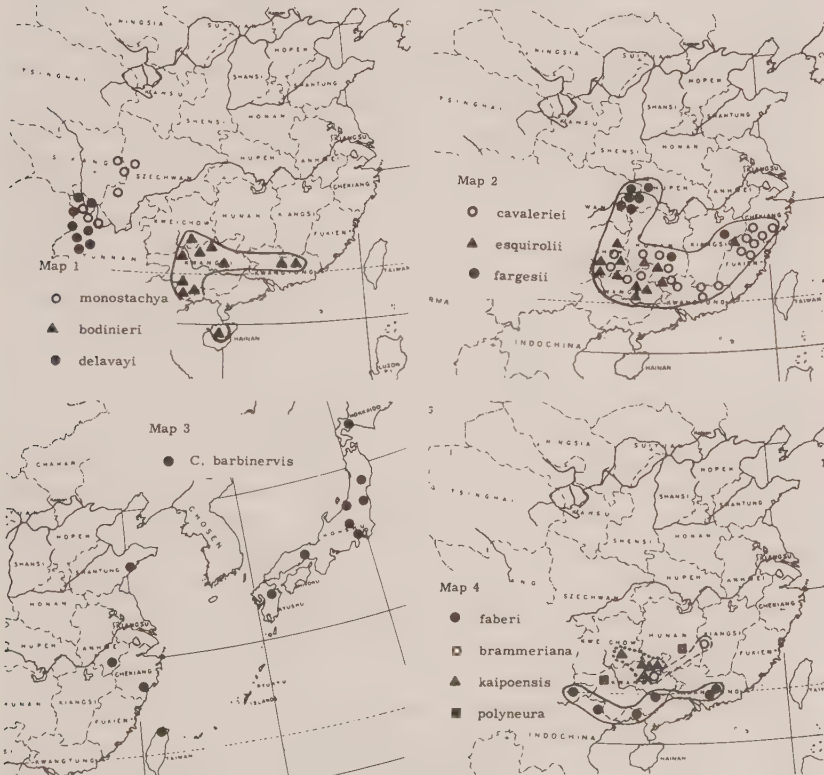
The eastern group involves a more heterogeneous assemblage of species.

The area covered by these species is at lower altitudes, the majority of the species occurring between 600 and 1000 meters above sea level. A couple of species may reach an altitude of 1250–1600 meters. *Clethra kaipoensis* has been collected at altitudes of 1000–2100 meters.

The distribution maps of different species involved in the eastern region indicate that the Nan-ling Range constitutes the center of the aggregation of species. This range represents a chain of much-dissected ancient hills and mountains extending along the Tropic of Cancer from the Yun-nan-Kwangsi border, eastward to the Kweichow-Hunan-Kwangsi-Kwangtung borders, and then northeastward to the Kiangsi-Fukien-Chekiang borders.

Clethra bodinieri, the only species of section *Monostigma*, occurs principally on the southern flank of the Nan-ling Range, and from the western end, its range extends southward to Hainan (MAP 1).

The distributions of three closely related species, *C. cavaleriei*, *C. esquirolii* and *C. fargesii*, form a U-shaped pattern with the base falling over the Nan-ling Range, the left arm extending along the Kweichow-Hunan border northward to the Szechuan-Hupei border, and the right arm ex-



MAPS 1-4. Distribution of some Chinese species of *Clethra*.

tending along the Kiangsi-Fukien border northward to southern Chekiang (MAP 2). It is worthy of note that *C. fargesii* has its best development in the north on the western arm while *C. cavaleriei* is better developed in the north of the eastern arm.

MAP 3 shows the distribution of *C. barbinervis* in China and Japan. This species and *C. fargesii* are the eastern Asiatic representatives of series *Alnifoliae*. The other species of this series, *C. alnifolia* and *C. acuminata*, occur in eastern North America. The distribution of the species of *Clethra* in series *Alnifoliae* gives specific evidence to support the floristic relationship between the Lower Yangtze Region in China and eastern United States of America.

Clethra faberi is a unique species. In geographical distribution its range does not overlap that of any other Chinese species (MAP 4). In morphological characters it has the subcoriaceous leaves of the evergreen species in section *Monostigma*, the umbelliform-paniculate racemes and fringed petals of species in section *Cuellaria*, and the V-shaped anther of species in section *Clethra*. Evidently the distribution of *C. faberi* is on the northern periphery of the range of the series *Faberianae*. *Clethra petelotii* from Indochina, *C. lancifolia* from the Philippines, *C. canescens* from the Philippines, Borneo, and Celebes, and *C. ledermannii* from the western highlands of New Guinea are all related species.

The Chinese species of section *Cuellaria* are concentrated in a more limited area of the middle Nan-ling Range (MAP 4). It is noteworthy that all other species of this section are found in tropical America from Mexico to Brazil. In interpreting the distribution of the fresh-water fishes from tropical eastern Asia to the New World, Darlington in 1957 suggested that during different geological times, many kinds of fresh-water fishes evolved in the eastern Tethys region have radiated by way of the north temperate region to North and Central America. The distribution of *Clethra* in geological time probably followed the same direction.

Clethra is an Asiatic-American genus. It is evident that *C. arborea* Ait., the single species described from the Madeira Islands, is out of the natural range of the genus. A comparative study of all the material in the Gray Herbarium and the Arnold Arboretum reveals that *C. arborea* from the Madeira Islands is closely allied to *C. pulcherrima* of the east coast of Sumatra. The two species are alike in their arborescent habit, large, oblong-elliptic, pubescent leaves, paniculate racemes, large flowers, elongate petals, included stamens, hirsute filaments and V-shaped anthers. It is very clear that *C. arborea* is an introduction from the East Indies to the Madeira Islands in historical time. The small hairy capsules and the very minute seeds are adapted for attachment. It was probably accidentally introduced in connection with the spice trade, and was firmly established in the late eighteenth century when it first caught the attention of British naturalists. Both *C. pulcherrima* and *C. arborea* are closely related to *C. delavayi* of western China.

TAXONOMY

Clethra Linn. Sp. Pl. 396. 1753, Gen. Pl. ed. 5. 188. 1754; Benth. & Hook. f. Gen. Pl. 2: 603. 1876; Rehder, Bibl. Cult. Trees Shrubs 502. 1949.

TYPE SPECIES: *C. alnifolia* Linn.

Evergreen or deciduous trees or shrubs 1–18 m. high. Leaves alternate, simple, exstipulate, chartaceous, rarely coriaceous or subcoriaceous, obovate, oblong, rarely lanceolate, base cuneate, rarely acute or rounded, apex acuminate, margin serrate, rarely subentire. Flowers in simple, paniculate, or subumbelliform racemes, rachis and pedicels stellate-pubescent, rarely covered by simple, straight hairs; calyx patelliform, with broad-ovate to lanceolate lobes; corolla choripetalous, emarginate, erose or fringed; stamens 10, in two whorls, the outer whorl opposite the petals, filaments glabrous or hirsute, reflexed in bud, straightened at anthesis, anthers 4-celled in bud, at anthesis V-shaped, oblong-obovate or obcordate, connective extending into a basal sterile process, thecae opening by terminal rimiform pores; pollen grains simple, tricolporate or triplicate; ovary superior, pubescent, 3-locular, style trifid or undivided, 3-lobed or not lobed; stigmas 3, rarely 1; ovules 20–40 in each locule, on axile placentas. Fruit a subglobose capsule with persistent calyx and style, loculicidal. Seeds small, ovoid and irregularly angular or dorso-ventrally compressed, the seed coat of one layer of cells, extremely reticulate, in some species wing-like; endosperm fleshy and oily. About 120 species with Asian-American distribution.

KEY TO THE SECTIONS, SERIES AND SPECIES

- A. Petals densely barbate on the inside; style undivided; stigma 1, punctiform; fruits globose, villose-hirsute; leaves evergreen; pollen triplicate; hairs on the rachis and pedicels simple, gray, appressed. Sect. 1. MONOSTIGMA. 1. *C. bodinieri*.
- A. Petals glabrous or sparsely villose at the base on the inside; style trifid or undivided, 3-lobed with 3 stigmas; leaves deciduous (except *C. smithiana*); pollen tricolporate; hairs on the rachis and pedicels stellate or tufted, hirsute, usually ferrugineous.
- B. Anthers V-shaped or oblong-obovate; pedicels longer than the sepals at anthesis; petals emarginate, rarely fringed; racemes various. Sect. 2. CLETHRA.
- C. Flowers large, the petals 8–10 mm. long; stamens included; filaments hirsute, the hairs white; anthers oblong-ovate; racemes solitary. Series A. DELAVAYANAE.
- D. Style pubescent; petals papillose on the outside; leaves elliptic, attenuate at both ends, 6–14 cm. long, 2.5–5.5 cm. wide. 2. *C. monostachya*.
- D. Style glabrous; petals smooth outside; leaves various in shape and size.
- E. Leaves uniformly hispid above, pubescent beneath (except the

- glabrous variety), obovate or oblong, 7–23 cm. long, 3.5–9 cm. wide. 3. *C. delavayi*.
- E. Leaves glabrous above, inconspicuously appressed-pilose on the midrib and lateral nerves beneath, lanceolate, 10–15.5 cm. long, 3–4 cm. wide. 4. *C. yuiana*.
- C. Flowers small, the petals 4–6 mm. long; stamens exserted, the filaments glabrous or villose with ferrugineous or nigrescent hairs; racemes various.
- F. Racemes solitary; sepals ovate-lanceolate, 4–5 mm. long; petals emarginate; anthers V-shaped, 3 mm. long. Series B. ESQUIROLIANAE.
- G. Filaments glabrous; petals not glaucous; leaves oblong-elliptic, the base acute or obtuse. 5. *C. cavaleriei*.
- G. Filaments pubescent; basal half of the petals glaucous; leaves ovate-elliptic, the base obtuse or rounded. 6. *C. esquirolii*.
- F. Racemes paniculate or subumbelliform; sepals ovate-orbicular, 2–4 mm. long; petals more or less fringed. Series C. ALNIFOLIAE.
- H. Fruiting pedicels 2–3 times as long as the diameter of the capsules; leaves chartaceous.
- I. Filaments glabrous; leaves obovate or broad-elliptic, the base cuneate; racemes paniculate; sepals broad-ovate, 2–2.5 mm. long, obtuse. 7. *C. barbinervis*.
- I. Filaments pubescent; leaves ovate-oblong, the base obtuse; racemes subumbelliform; sepals lanceolate, 4–5 mm. long. 8. *C. fargesii*.
- H. Fruiting pedicels about as long as the diameter of the capsules; leaves subcoriaceous. Series D. FABERIANAE.
9. *C. faberi*.
- B. Anthers cordate; pedicels shorter than the sepals at anthesis; petals fringed; racemes subumbelliform. Sect. 3. CUELLARIA.
- J. Style pubescent near the base. 10. *C. pinfaensis*.
- J. Style glabrous.
- K. Leaves deciduous, distinctly serrate, elliptic or oblong, chartaceous, 11–20 cm. long; 5–7 cm. wide; petals glabrous.
- L. Primary lateral nerves parallel-arcuate, 6–10 mm. apart; hairs on the lower leaf-surface or nerves stellate.
- M. Filaments glabrous.
- N. Leaves stellate-hirsute on the nerves beneath, otherwise glabrous; margin sharply serrate. 11. *C. kaipoensis*.
- N. Leaves uniformly velvety beneath; margin subentire, minutely mucronulate-ciliate or serrate. 12. *C. brammeriana*.
- M. Filaments villose at the base. 13. *C. kwangsiensis*.
- L. Primary lateral nerves parallel, 4–6 mm. apart; hairs on the nerves beneath simple, appressed. 14. *C. polyneura*.
- K. Leaves evergreen, subentire or remotely serrate near the apex, linear-lanceolate, 7–13 cm. long, 2–3 cm. wide. 15. *C. smithiana*.

Section 1. MONOSTIGMA S. Y. Hu

Clethra, sect. **Monostigma**, sect. nov.TYPE SPECIES: *C. bodinieri* Lévl.

Frutices sempervirentes ramulosis hornotinis pilosis; foliis coriaceis; racemis solitariis, rachibus pedicellisque pilosis; sepalis ovatis; petalis intus barbatis, filamentis hirsutis; stylis glabris, apice punctiformibus. One species, Kwangtung, Kwangsi, Hainan and Kweichow.

1. **Clethra bodinieri** Lévl. Repert. Sp. Nov. Fedde 10: 475. 1912; Hand.-Mazz. Sinensia 5: 3. 1934; Merr. & Chun, Sunyatsenia 5: 156. 1940.

var. **bodinieri**

An evergreen shrub, 2–5 m. high, the branchlets ascending, the current year's growth 2–3 mm. thick, inconspicuously pilose, the hairs simple. Leaves coriaceous, lanceolate, 5–9 cm. long, 1–2.5 cm. wide, base cuneate to acute, apex caudate-acuminate, the acumen 1.5–2 cm. long, glabrous above, inconspicuously pilose on the midrib beneath, angles of principal nerves slightly barbate; margin mucronate-denticulate, the basal half or one-third entire, lateral nerves 8, arcuate, obscure above, conspicuous beneath; petioles 5–12 mm. long, pilose. Racemes solitary, 3–13 cm. long, peduncles distinct, rachis pilose, the hairs simple, gray; pedicels 7–8 mm. long at anthesis; sepals ovate, 2.5–3 mm. long; petals oblong, 5 mm. long, 2.5 mm. wide, densely barbate inside; filaments hirsute; style glabrous, the stigma entire. Capsules globose, densely villose-hirsute; persistent style 7–9 mm. long; pedicels 10–12 mm. long. Seeds brown, 0.5–1 mm. long, angular-ovoid.

KWANGTUNG: *W. T. Tsang* 25451, 25620, 25828. KWANGSI: *R. C. Ching* 5695, 5734, 5804, 7181; *W. T. Tsang* 22450, 24023; *C. Wang* 39602.

Occurring in open thickets or woods at altitudes of 600–1600 meters; the white flowers with pinkish sepals and pedicels appear in June; a very distinct species with no close relationship to any other Chinese species of *Clethra*.

var. **latifolia**, var. nov.

Frutex sempervirens 4 m. altus, ramulis hornotinis incanis; foliis obovato-oblongis vel obovato-ellipticis, 7–9.5 cm. longis, 2.5–3 cm. latis, basi obtusis, apice acuminatis, acumine 5–10 mm. longo, margine serratis, supra glabris, subtus barbatis; racemis 6 cm. longis; filamentis dense villosis; stylo glabro.

HAINAN: Loktung, in dense woods, *S. K. Lau* 27312 (type, A), June 27, 1936 (shrub 4 m. high, leaves green above).

Occurring in dense woods; flowering in late June; distinguished from the typical *C. bodinieri* by its obovate-oblong leaves with obtuse bases.

var. *parvifolia*, var. nov.

Frutex 1.5–2.5 m. altus ramulis hornotinis sparse pilosis; foliis ellipticis, raro obovato-ellipticis, 3–5 cm. longis, 8–17 mm. latis, basi cuneatis et acutis, apice acuminatis, acumine 5–9 mm. longo, supra glabris, subtus barbatis aliter glabris; racemis 6–9 cm. longis; filamentis hirsutis; stylo glabro.

KWANGSI: Shang-sze District, fairly common, in thickets, dry steep slope, *W. T. Tsang* 22450 (type, A), June 2–7, 1933 (woody, 5 ft. high, flowers white, fragrant); *W. T. Tsang* 23822, 22456.

Occurring in thickets and woods; flowering in early June; distinguished from the typical *C. bodinieri* by its small leaves which seldom reach 5 cm. in length.

Section 2. CLETHRA

Clethra, sect. Clethra

Clethra sect. *Euclethra* DC. Prodr. 7: 588. 1839; Drude in Engler & Prantl, Pflanzenfam. IV. 1: 1. 1897.

TYPE SPECIES: *C. alnifolia* Linn.

Deciduous trees or shrubs, branchlets stellate-pilose. Leaves chartaceous, rarely subcoriaceous. Rachis and pedicels stellate-pilose; racemes solitary or paniculate or subumbelliform, pedicels elongate; sepals ovate to lanceolate; petals glabrous inside or rarely slightly pilose near the base; style trifid or undivided and 3-lobed at the apex, stigmas 3. About 15 species, eastern Asia and eastern North America. Subdivided into four series.

Series A. DELAVAYANAE S. Y. Hu

Clethra, sect. Clethra, series Delavayanae, ser. nov.

TYPE SPECIES: *C. delavayi* Franch.

Arbores vel frutices, foliis chartaceis, serrato-dentatis; racemis solitariis, pedicellis elongatis; staminibus inclusis, filamentis hirsutis; stylis trifidis; capsulis hispidis; seminibus dorso-ventralibus compressis. Three species in West China, the related species in Sumatra.

2. *Clethra monostachya* Rehder & Wilson in Sargent, Pl. Wils. 1: 501. 1913; Rehder, Man. 675. 1927, ed. 2. 690. 1940, Bibl. 502. 1949; Chen, Ill. Man. Chin. Trees Shrubs 942. 1937.

Clethra delavayi sensu Stapf in Bot. Mag. 148: t. 8970. 1923; sensu Rehder, Man. 675. 1927, ed. 2. 690. 1940, non Franchet.

A tall shrub or small tree, 2–8 m. high. Leaves elliptic, or ovate-elliptic, rarely lanceolate, 7–13 cm. long, 2.5–5.5 cm. wide, base cuneate, apex acuminate, acumen 1–1.5 cm. long, apiculate, margin sharply serrate,

primary lateral nerves 16–21 pairs, both surfaces glabrous, the large nerves slightly pilose and their angles barbate beneath; petioles 1–2.5 cm. long, inconspicuously stellate-pilose in the grooves above; leaves produced by active lateral buds lanceolate, 4–6.5 cm. long, 1.3–2 cm. wide, both surfaces subglabrous, the nerves and their angles pilose beneath. Racemes solitary, 7–18 cm. long, the rachis densely ferrugineous-hirsute, the hairs tufted; pedicels 6–10 mm. long at anthesis; sepals 4–5 mm. long, acute; petals 5–6 mm. long, papillose outside; filaments hirsute; style pubescent, apex 3-cleft. Capsules subglobose, 4 mm. in diameter; pedicels 15–18 mm. long; persistent style 7–8 mm. long.

YUNNAN: *R. C. Ching* 21452; *M. K. Li* 2079; *T. T. Yu* 17303. SIKANG (Szechuan on labels): Tien-chuan, *Y. S. Liu* 1329; Han-Yuen, Ta Hsiang Ling, *C. Y. Chiao* 1616; Moupin, *E. H. Wilson* 1192 (paratype). West China, without precise locality, *E. H. Wilson*, Veitch Exp. 3927 (type).

Occurring on the margins of woods and thickets at altitudes of 1700–2800 meters in the mountains of the Yunnan-Szechuan-Sikang borders; a very distinct species closely related to *C. delavayi*; distinguished by its elliptic leaves attenuate at both ends, smaller flowers, papillose petals, pubescent filaments and styles.

The specimens from Yunnan are not typical. The stamens are enclosed, as in *C. delavayi*. The material illustrated by Stapf has pilose styles, and it apparently belongs here. Rehder's account in his *Manual* is based on Stapf's illustration. The isotype of *C. delavayi* has glabrous styles.

3. *Clethra delavayi* Franchet, Jour. de Bot. 9: 370. 1895; P. Dop, Bull. Soc. Bot. France 75: 731. 1928; Rehder, Man. 675. 1927, ed. 2. 690. 1940. Bibl. 502. 1949; Chen, Ill. Man. Chin. Trees Shrubs 942. 1937; Merr. in Brittonia 4: 137. 1941.

var. *delavayi*

A tall shrub or small tree 4–5 m. tall, the current year's growth densely stellate-hispid, 3–6 mm. thick. Leaves obovate or elliptic-oblong, 7–15 cm. long, 3.5–6 cm. wide, base cuneate, apex acuminate or acute, the acumen 5–10 mm. long, uniformly hispid above, tomentose beneath, margin serrate, lateral nerves 20 or 21 pairs; petioles 10–17, densely villose; axillary buds more or less stalked, usually bearing no leaves, the stalk 3–40 mm. long. Racemes solitary, 18–25 cm. long, the rachis densely ferrugineous-hispid, the hairs tufted; pedicels 6–7 mm. long at anthesis; sepals ovate-lanceolate, 5–6 mm. long; petals oblong-obovate, 10 mm. long, 5 mm. wide, apex emarginate, ciliate; filament hirsute at the base, the hairs white; style glabrous, the apex trifid. Capsules subglobose, 4 mm. in diameter; persistent style 6–7 mm. long; pedicels 14–20 mm. long.

YUNNAN: *Delavay* 3319 (isotype); *G. Forrest* 11590, 15528, 15839, 17545; *McLaren* (*C Collector* 237); *H. T. Tsai* 58408; *T. T. Yu* 20979.

Occurring in mixed forest at altitudes of 2400–3200 meters; a very distinct species, closely related to *C. monostachya*, distinguished by its obovate leaves which are uniformly tomentose beneath, large flowers with enclosed anthers, hispid filaments, and glabrous styles.

var. lanata, var. nov.

Arbor parva 4 m. alta; foliis obovatis vel oblango-ellipticis, 11–12 cm. longis, 3.5–5.5 cm. latis, supra hispidis, subtus dense lanatis; pedicellis fructuum 1.5–2 cm. longis.

YUNNAN: Che-tse-lo, Pi-lo-shan, alt. 4000 m., *H. T. Tsai* 58263 (type, A), August 27, 1934 (tree, flower white); *H. T. Tsai* 58459.

This variety occurs in the forest of Che-tse-lo of western Yunnan. The dense-lanate lower leaf-surface is very distinctive.

var. glabra, var. nov.

Arbor parva 3–5 m. alta; foliis oblango-ellipticis vel obovato-oblongis, 13–23 cm. longis, 5.5–9 cm. latis, supra glabris, subtus glabrescentibus, ad costam et nervos lateralibus sparse pilosis; pedicellis florum 8–15 mm longis.

YUNNAN: *R. C. Ching* 20478, 22107; *K. M. Feng* 3301; *G. Forrest* 8875; *McLaren* (*D Collector* 130); *J. F. Rock* 17111, 18461; *H. T. Tsai* 59905, 59951; *C. W. Wang* 63886, 68702; Wei-Hsi, Mount Shang-Ma-Kou, alt. 3400 m., *J. F. Rock* 17174 (type, A), August 1928 (tree, 3–5 m. high, flowers white).

Occurring in mixed forests by streams at altitudes of 2800–3800 meters; the white flowers open in August; distinguished by its leaves which are glabrous above and pilose beneath on the principal nerves only.

4. Clethra yuiana, sp. nov.

Arbor 7–10 m. alta, ramulis hornotinis 4 mm. diametro, glabrescentibus; foliis lanceolatis, 10–15.5 cm. longis, 3–4 cm. latis, utrinque acuminate, acumine 1 cm. longo, margine mucronato-serratis, supra glabris; subtus ad nervos primarios et costam pilosis, aliter glabris, nervis lateralibus utrinque 22–24, foliis ramulorum axillarium ellipticis vel lanceolatis, 1.5–2.5 cm. longis, 6–8 mm. latis, utrinque praesertim ad nervos pilosis; racemis solitariis, 22 cm. longis, densifloribus; rachibus stellato-pilosis, pilis brevibus; pedicellis florum 8–10 mm. longis; sepalis ovato-lanceolatis 5–6 mm. longis; petalis obovatis, 8 mm. longis, 5–6 mm. latis, apice emarginatis, utrinque glabris; filamentis hirsutis; stylis glabris, apice trifidis; capsulis ignotis.

YUNNAN: Shunning, Hila, Wumlung, alt. 2750 m., among forest, common, *T. T. Yu* 1720 (type, A), July 13, 1938 (tree, 20–30 ft. high, flowers white).

Occurring frequently in mixed forest at an altitude of 2750 meters; flowering in mid-July; closely related to *C. monostachya*, but distinguished by its larger flowers and glabrous styles.

Series B. ESQUIROLIANAE S. Y. Hu

Clethra, sect. **Clethra**, series **Esquirolianae**, ser. nov.TYPE SPECIES: *C. esquirolii* Lévl.

Frutices foliis ellipticis vel ovato-ellipticis, chartaceis, arguto-serratis; racemis solitariis, pedicellis elongatis; sepalis lanceolatis, staminibus exsertis, antheris V-formibus, elongatis; seminibus ovoideo-polygonis. Two species, southeastern China.

5. **Clethra cavaleriei** Lévl. Repert. Sp. Nov. Fedde 10: 476. 1912; Rehder, Jour. Arnold Arb. 15: 267. 1934; Hand.-Mazz. Beih. Bot. Centralbl. 56B: 449. 1937.

Clethra lineata Lévl. Repert. Sp. Nov. Fedde 12: 534. 1913.

Clethra longebracteata Sleumer, *ibid.* 38: 205. 1935.

Clethra sinica Hao, *ibid.* 42: 85. 1937.

A shrub or small tree 1–5 m. high, the current year's growth densely pilose, the hairs short-stellate. Leaves elliptic, 6–10 cm. long, 1.5–4 cm. wide, base acute, apex acute or shortly acuminate, glabrous above, very sparsely pilose on the principal nerves beneath, margin serrate, lateral nerves 12 or 13 pairs, reticulations of veinlets distinct beneath; petioles 1–1.5 cm. long, appressed pilose and glabrescent; leaves produced by active axillary buds lanceolate, 2–7 cm. long, 1–1.5 cm. wide, both surfaces sparsely stellate-pilose. Racemes solitary, 9–15 cm. long, bracts longer than the pedicels; pedicels 7–10 mm. long at anthesis; sepals lanceolate, 5 mm. long; petals 6 mm. long; filaments glabrous; style glabrous, the apex trifid. Capsules subglobose, 4–5 mm. in diameter; persistent style 9 mm. long; pedicels 14–15 mm. long.

FUKIEN: *R. C. Ching* 2250, 2300; *H. M. Fan* 9474, 9493, 9515; *H. H. Chung* 2923. KWANGTUNG: *R. Mell* 883; *W. T. Tsang* 21413, 21661. KWANGSI: *S. K. Lau* 28753, 28755. CHEKIANG: *R. C. Ching* 2101; *Y. L. Keng* 164 (isosyntype of *C. sinica*), 175 (isotype of *C. longebracteata*). KWEICHOW: *J. Cavalerie* 5 (fragment and photo of type); *J. Esquirol* 3238 (photo and fragment of type of *C. lineata*); *Handel-Mazzetti* 172 = 10557. HUNAN: *Fan & Li* 253.

Occurring in woods and thickets at altitudes of 780–1250 m.; flowering in August; closely related to *C. esquirolii*, distinguished by its glabrous filaments.

6. **Clethra esquirolii** Lévl. Repert. Sp. Nov. Fedde 10: 475. 1912.

Clethra cavaleriei sensu Rehder, Jour. Arnold Arb. 15: 267. 1934, p.p.; sensu Hand.-Mazz. Symb. Sin. 7: 760. 1936, p.p., non Lévl.

A shrub 1–3 m. high, current year's growth sparsely stellate-pilose, 3–4 mm. in diameter, subterete or angular. Leaves ovate-elliptic or elliptic, 6.5–10 cm. long, 2.5–4.5 cm. wide, base obtuse or rounded, apex short-acuminate, the acumen 1 cm. long, glabrous above, the nerves sparsely pilose and their angles slightly barbate beneath, margin serrate.

lateral nerves 10–12 pairs; petioles 1–2 cm. long, hirsute, straight and stellate hairs intermixed; leaves produced on active axillary buds elliptic, 3–4.5 cm. long, 12–15 mm. wide, both surfaces stellate-pilose, the midrib and lateral nerves lanate beneath. Racemes solitary, 10–16 cm. long, the rachis ferrugineously stellate-hirsute; pedicels 9–11 mm. long at anthesis; sepals ovate-lanceolate, 4–5 mm. long; petals oblong, 6–7 mm. long, 3–4 mm. wide, sparsely villose inside, basal half glaucous outside; filaments villose, the hairs ferrugineous or nigrescent; style glabrous, trifid at the apex. Capsules subglobose, 4 mm. in diameter; pedicels 1.5–2 cm. long; persistent style 9–12 mm. long.

FUKIEN: *R. C. Ching* 2300. KWANGTUNG: Lokchong, *Y. Tsiang* 1422. KWANGSI: Ling-Chuan, *W. T. Tsang* 27871; Tzu-yuen, *T. S. Tsoong* (= *Z. S. Chung*) 83440; *C. Wang* 39565, 40068. HUNAN: Sinning, *Fan & Li* 453; Wu-kang, *Handel-Mazzetti* 842 = 12397. HUPEI: *A. Henry* 2838. KWEICHOW: *J. Cavalerie*, July 19, 1898; *J. Cavalerie* 69 (*E. Bodinier*); *J. Esquirol* 651 (type, fragment and photo); *Steward, Chiao & Cheo* 394; *Y. Tsiang* 5460.

Occurring in open ridges or ravines of the Nan-ling Range, its range extending from northern Kwangsi and Kweichow, eastward through Hunan to northern Kwangtung and northern Fukien, and northward to western Hupei; closely related to *C. cavaleriei*, distinguished by its ovate or ovate-elliptic leaves with obtuse or rounded base, its glaucous petals and pubescent filaments.

Rehder and Handel-Mazzetti both interpreted this species as synonymous with *C. cavaleriei*. The fragment of the type of *C. esquirolii* and *Handel-Mazzetti* 12397 both have pubescent filaments. In this respect, they are different from the type of *C. cavaleriei*. *Clethra esquirolii* is distinguished from *C. fargesii* by its larger flowers and solitary racemes.

Series C. ALNIFOLIAE S. Y. Hu

Clethra sect. *Clethra*, series *Alnifoliae*, ser. nov.

TYPE SPECIES: *C. alnifolia* L.

Frutices foliis chartaceis, obovatis vel lato-ellipticis, crasso-serratis; racemis paniculatis; staminibus exsertis, antheris V-formibus; seminibus polygonis vel compressis. Five species, eastern United States of America and the Lower Yangtze Region of China.

7. *Clethra barbinervis* Sieb. & Zucc. *Abh. Phys.-Math. Cl. Akad. Wiss. München* IV. 3: 128. 1846; Gilg, *Bot. Jahrb. Engler* 34 (Beibl. 75): 56. 1904; Loes. in *Beih. Bot. Centralbl.* 37(2): 164. 1919; Rehder, *Man.* 1927, ed. 2. 690. 1940, *Bibl.* 502. 1949; Kai, *Pl. Sin.* Ill. 306. fig. 538. 1937.

A shrub up to 10 m. high, the current year's growth 3–4 mm. thick, subglabrescent or minutely stellate-pilose. Leaves obovate-elliptic, 7–14 cm. long, 3–6.5 cm. wide, base cuneate and acute, apex abruptly short-

acuminate, the acumen deltoid, 5–10 mm. long, glabrous above, midrib and principal nerves hirsute and their angles barbate beneath, the hairs simple; margin sharp-serrate; lateral nerves 12–14 pairs, arcuate; petioles 1–2.5 cm. long, pilose, the hair appressed; leaves produced by active axillary buds obovate, 3.5–6.5 cm. long, 1.5–2.5 cm. wide, sparsely stellate-pilose above, sparsely villose beneath, straight and stellate hairs intermixed. Racemes 3–6, paniculate, the rachis densely ferrugineous-hispid, the hairs tufted; pedicels 4–6 mm. long at anthesis; sepals sub-orbicular-ovate, 2–2.5 mm. long; petals obovate, 5–6 mm. long, 3–4 mm. wide; apex emarginate, and fringed; filaments glabrous; style glabrous, the apex trifid. Capsules subglobose, 4 mm. in diameter; persistent style 6–8 mm. long; pedicel 6–8 mm. long.

TAIWAN: *R. Kanehira*, Sept. 5, 1920. CHEKIANG: *R. C. Ching* 1642. ANHWEI: *R. C. Ching* 3237, 3277. SHANTUNG: Tsingtao, *Zimmermann* 432.

Occurring in thickets on open hills at an altitude of 1000 meters; related to *C. faberi* and *C. fargesii* through its paniculate inflorescences, short sepals, and fringed petals; distinguished from *C. faberi* by its obovate leaves and elongate pedicels and from *C. fargesii* by its glabrous filaments and obovate leaves cuneate at the base. Kanehira and Zimmermann's collections are out of the normal range of the species. Probably these collections were made from cultivated plants. This species is common in Japan, and it is most likely that this species was introduced into Tsingtao and Taiwan from Japan.

8. *Clethra fargesii* Franch. Jour. de Bot. 9: 369. 1895; Rehder & Wilson in Sargent, Pl. Wils. 1: 502. 1913; Rehder, Man. 674. 1927, ed. 2, 690. 1940, Bibl. 502. 1949; Chen, Ill. Man. Chin. Trees Shrubs 942. fig. 835. 1937.

Clethra canescens sensu Forbes & Hemsl. Jour. Linn. Soc. Bot. 26: 33. (Ind. Fl. Sin. II). 1889, non Reinw. ex Blume.

Clethra sleumeriana Hao, Repert. Sp. Nov. Fedde 42: 84. 1937.

A tall shrub up to 4 m. high, the current year's growth densely stellate-pilose, 3–5 mm. thick. Leaves ovate-elliptic, 7–14 cm. long, 3–5 cm. wide, base obtuse or rotundate, apex acuminate, the acumen 1–2 cm. long, glabrous above, along the midrib and the principal nerves stellate-villose and their angles barbate beneath, lateral nerves 16–17 pairs, arcuate; margin mucronate serrate; petioles 14–17 mm. long, sparsely stellate pilose; leaves produced by the active axillary buds lanceolate, 4–10 cm. long, 1.5–3.3 cm. wide, both sides stellate pubescent. Racemes 3–7, subumbelliform-paniculate, the rachis densely brown-hirsute, the hairs tufted; pedicels 6–10 mm. long at anthesis; sepals lanceolate, 4–5 mm. long; petals obovate, 5–6 mm. long; filaments hirsute near the base; style glabrous, the apex trifid. Capsules subglobose, 3 mm. in diameter; persistent style 5 mm. long; pedicels 12–13 mm. long.

KIANGSI: *H. H. Hu* 1320. HUPEI: *Cheng & Hwa* 821, 1068, 1110; *H. C.*

Chow 885, 1178; *W. Y. Chun* 3714, 3734; *A. Henry* 5818, 6407, 7220; *E. H. Wilson* (Veitch Exp.) 1326, 2222. HUNAN: *S. S. Sin* 615 (type of *C. sleumeriana*. Hao, not seen). SZECHUAN: *Farges* 108 (type, not seen).

Common in open woodlands and thickets in the middle Yangtze Region; closely related to *C. esquirolii*, but distinguished by its umbelliform-paniculate racemes, smaller flowers and densely stellate-pubescent branchlets.

Series D. FABERIANAE S. Y. Hu

Clethra, sect. **Clethra**, series **Faberianae**, ser. nov.

TYPE SPECIES: *C. faberi* Hance.

Frutices foliis subcoriaceis, subglabris vel subtus stellato-pilosis, canescentibus, serratis; racemis subumbelliformibus, pedicellis brevibus; petalis fimbriatis. About 10 species, China, Indo-China, the Philippines, Borneo, Celebes and New Guinea.

9. **Clethra faberi** Hance, Jour. Bot. Brit. For. 21: 130. 1838, "*fabri*"; Merr. Philipp. Jour. Sci. Bot. 13: 154. 1918; P. Dop, Bull. Soc. Bot. France 75: 732. 1928.

Clethra canescens sensu Forbes & Hemsl. Jour. Linn. Soc. Bot. 26: 33. (Ind. Fl. Sin. II). 1889, p.p.; sensu Dunn & Tutchner, Kew Bull. Add. Ser. 10: 155. (Fl. Kwangt. Hongk.) 1912, non Reinw.

Clethra liangii Li, Jour. Arnold Arb. 24: 449. 1943.

A deciduous shrub 2–2.5 m. high, the current year's growth sparsely pilose or glabrescent, 3 mm. in diameter. Leaves subcoriaceous, elliptic, or obovate-elliptic, rarely oblanceolate, 6–11 cm. long, 2–3.2 cm. wide, base acute, apex acuminate, the acumen 1 cm. long, margin sharply serrate, primary lateral nerves 10 or 11 pairs, parallel-arcuate, 6–8 mm. apart, impressed above, reticulations of the veinlets distinct beneath, lamina glabrous on both surfaces, on the principal nerves very sparsely pilose beneath; petioles 6–8 mm. long, sparsely stellate pilose; leaves produced by active axillary buds elliptic, 2.5–8 cm. long, 1–2.5 cm. wide, glossy, glabrous above, hispid on the nerves beneath. Racemes 2–7, paniculate, rarely on weak branchlets solitary, densely and ferrugineously caespitose-hirsute; many bracts persistent; pedicels 3–4 mm. long; sepals suborbicular-ovate, 2.5–3 mm. long, apex obtuse, mucronate; petals 4 mm. long, 2 mm. wide, inside sparsely villose below the middle; filaments glabrous, anthers acute at the base, divergent at the apex; style glabrous, 4 mm. long after anthesis, the apex subcapitate, lobed or shallowly cleft. Capsules 2.5 mm. in diameter.

KWANGTUNG: *C. Ford* 56; *W. T. Tsang* 26761. KWANGSI: *H. Y. Liang* 69645 (type of *C. liangii*); *S. P. Ko* 55527. YUNNAN: *H. T. Tsai* 60876.

Occurring in densely shaded forest or on open, grassy slopes at altitudes of 970–1100 meters; the white flowers appearing in late July and early

August; a very distinct species. Its short, obtuse sepals suggest a relationship with *C. barbinervis*, but its short pedicels, subcoriaceous leaves and small anthers are very different. The isosyntypes of *C. annamensis* P. Dop (*M. Poilane* 7519, 7616) apparently belong here.

Section 3. CUELLARIA (Ruiz & Pav.) DC.

Clethra, sect. **Cuellaria** (Ruiz & Pav.) DC. Prodr. 7: 589. 1839.

Cuellaria Ruiz & Pav. Fl. Per. Chil. Prodr. 59. t. 10. 1794, Syst. Veg. 103. 1798.

TYPE SPECIES: *C. ferruginea* Ruiz & Pav.

Trees or shrubs, branchlets densely stellate-pubescent. Leaves coriaceous or chartaceous. Rachis and pedicels densely ferrugineous-stellate-pubescent; racemes paniculate or subumbelliform, pedicels very short; sepals oblong or ovate; petals erose or fimbriate; stamens exserted or included. Seeds winged, or polygonous. About 85 species, chiefly in tropical America, 4 in China.

10. **Clethra pinfaensis** Lévl. Repert. Sp. Nov. Fedde 10: 476. 1912.

Clethra kaipoensis sensu Rehder, Jour. Arnold Arb. 15: 268. 1934; sensu Hand.-Mazz. Symb. Sin. 7: 760. 1926, non Lévl.

A tree up to 13 m. high, the trunk 30 cm. in diameter, the bark smooth, brownish. Leaves oblong-elliptic, 8–15 cm. long, 3–5 cm. wide, base obtuse, apex acuminate, the acumen 1.5–2 cm. long, margin sharp-serrate; primary lateral nerves 14 or 15 pairs, parallel-arcuate, glabrous above, glabrescent beneath, the hairs on the nerves beneath simple, appressed; petioles 8–20 mm. long; leaves produced by active axillary buds 3–7.5 cm. long, 1.5–2.5 cm. wide, sparsely stellate-pubescent above. Racemes 4–6, subumbellate, 14–18 cm. long, rarely shorter, densely ferrugineous-hirsute, the hairs tufted; pedicels 2–3 mm. long at anthesis; sepals ovate, 2–3 mm. long; petals 4 mm. long, 2 mm. wide; filaments glabrous; style pubescent at the basal end. Capsules 3 mm. in diameter; fruiting pedicels 4 mm. long; persistent style 5–6 mm. long, the stigma trifold. Seeds varying in size and shape, compressed ovoid, triangular, or subcylindric, 1–1.5 mm. long, 0.5–1 mm. wide, reticulate, brownish.

KWANGSI: *R. C. Ching* 6026, 7000, 7116. KWEICHOW: *J. Cavalerie* 346 (photo and fragment of type); *Handel-Mazzetti* 254 = 10766, 325 = 10997.

Occurring in woods at altitudes of 1300–1500 meters; flowering in late July and early August; closely related to *C. kaipoensis*, but distinguished by its styles being pubescent near the base. The style-character is clear in the fragment of the type. When Rehder and Handel-Mazzetti interpreted *C. pinfaensis* and *C. kaipoensis* as conspecific, they ignored this distinct character.

11. *Clethra kaipoensis* Lévl. Repert. Sp. Nov. Fedde 10: 475. 1912; Rehder, Jour. Arnold Arb. 15: 268. 1934, p.p.

A deciduous shrub 1–3 m. high. Leaves oblong-elliptic, 13–19 cm. long, 4–9 cm. wide, base obtuse or rotund, apex acuminate, the acumen 2 cm. long, margin coarse- and sharp-serrate, primary lateral nerves 16–18, 7–13 mm. apart, glabrescent above, sparsely stellate-pubescent along the nerves and barbate in their angles beneath; petioles 1.5–2.5 cm. long, densely ferrugineous-hirsute; leaves produced by the active axillary buds broad elliptic, 3–4 cm. long, 1.5–2 cm. wide, densely velvety on both surfaces, the hairs stellate. Racemes 4–8, subumbellate, occasionally solitary on weak branchlets, densely golden villose-hirsute; pedicels 3 mm. long; sepals deltoid-ovate, 3–4 mm. long; petals 4–5 mm. long; filaments glabrous, anthers 1.5 mm. long, base obtuse; style glabrous, the apex slightly enlarged, 3-lobed, after anthesis 5–6 mm. long. Capsule 4 mm. in diameter.

KWANGSI: *Steward & Cheo* 958; *Y. W. Taam* 24; *W. T. Tsang* 27900, 27916, 28425. KWEICHOW: *J. Cavalerie* 1221 (holotype, photo and fragment).

Occurring in forest at altitudes of 1000–2100 meters in Kweichow and northern Kwangsi; closely related to *C. kwangsiensis*; distinguished by its unusually large leaves and its glabrous filaments.

12. *Clethra brammeriana* Hand.-Mazz. Anzeig. Akad. Wiss. Wien Math.-Nat. Kl. 58: 151. 1921, Symb. Sin. 761. 1936.

A deciduous tree, the branchlets densely ferrugineous-hirsute, the hairs tufted, current year's growth 5 mm. in diameter. Leaves oblong-elliptic or obovate-oblong, 11–15 cm. long, 4.5–8 cm. wide, base obtuse or rotundate, apex acute or shortly acuminate, margin subentire and minutely mucronulate-ciliate or aristate-serrate, glabrous above, evenly velvety beneath, primary lateral nerves 15 or 16, parallel-arcuate, 8–12 mm. apart; petioles 14–18 mm. long, ferrugineously or castaneously hirsute. Racemes 5–13, subumbelliform-paniculate, 10–18 cm. long, densely and ferrugineously lanate-hirsute, some bracts persistent; pedicels 2 mm. long, sepals ovate-deltoid, 3–5 mm. long; petals 4 mm. long, 2.5 mm. wide; filaments glabrous, anthers obcordate, exserted; style 5 mm. long after anthesis, the apex undivided, 3-lobed. Fruit and seed not known.

KIANGSI: *T. H. Wang* 247 (isotype). KWANGSI: *T. S. Tsoong* (= *Z. S. Chung*) 83414.

Occurring in woods along ravines at an altitude of 600 meters; closely related to *C. kaipoensis*, but distinguished by its uniformly velvety lower leaf-surfaces. The flowers of *Tsoong* 83414, collected on July 15, are in very young bud.

13. *Clethra kwangsiensis*, sp. nov.

Arbor, ramulis hornotinis teretibus, 5 mm. diametro, dense ferrugineo-

pubescentibus pilis stellatis; foliis chartaceis, ovato-ellipticis, 16–17 cm. longis, 6–7.5 cm. latis, basi rotundatis vel obtusis, apice acuminatis, acumine 2 cm. longis, margine serratis, nervis lateralibus utrinque 20, arcuatis, supra glabris, subtus sparse stellato-pilosis, ad nervis villosis; petiolo 1.5 cm. longo, dense hirsuto; foliis ramulorum axillarium breviter ellipticis, 5–5.9 cm. longis, 3 cm. latis, utrinque stellato-tomentosis, pilis supra rigidis; racemis 6, subumbelliformi-paniculatis, 15–17 cm. longis, dense ferrugineis, pilis stellatis; pedicellis 2–4 mm. longis; sepalis deltoideo-ovatis, 3.5–4 mm. longis, acutis; petalis 5 mm. longis, 2 mm. latis, fimbriatis; filamentis villosis; stylo glabro, apice trifido; capsulis ignotis.

KWANGSI: Tzu Yuen District, in woods near a stream, *T. S. Tsoong* (= *Z. S. Chung*) 83570 (type, A), August 6, 1937 (tree, flowers white).

Occurring in woods along a stream; the white flowers appearing in early August; closely related to *C. kaipoensis*, but distinguished by its filaments being villose on the basal half.

14. *Clethra polyneura* Li, Jour. Arnold Arb. 24: 449. 1943.

Trees up to 18 meters high. Leaves oblong-lanceolate or oblong-elliptic, 9–15 cm. long, 3–6 cm. wide, base obtuse or rotund, apex acuminate, the acumen 1–2 cm. long, margin densely serrate, principal lateral nerves 18–25 pairs, parallel, 4–6 mm. apart, glabrous above, glabrescent beneath, the midrib and primary nerves sparsely pilose, the hairs simple and appressed; petioles 1–2.5 cm. long, sparsely stellate-hirsute; leaves produced by active axillary buds lanceolate, 4–7 cm. long, 1.3–2 cm. wide, sparsely stellate above, only the nerves ferrugineously stellate-pubescent beneath. Racemes 6–8, subumbellate-paniculate, 10–14 cm. long, densely ferrugineous-hirsute, the hairs tufted; pedicels 1.5–2 mm. long at anthesis; sepals ovate, acute, 2–3 mm. long; petals 3 mm. long, 1.75 mm. wide; filaments glabrous; style glabrous. Capsules 3 mm. in diameter, pericarp velvety; persistent style 6 mm. long, glabrous; fruiting pedicels 3–4 mm. long. Seed ovoid, reticulate, 1 mm. long, 0.5 mm. wide.

KWANGSI: *S. K. Lau* 28767 (type). HUNAN: *Fan & Li* 519.

Occurring on hilly slopes at altitudes of 650 m.; closely related to *C. kaipoensis*, but distinguished by its glabrous style and numerous parallel lateral nerves.

15. *Clethra smithiana* Fang, Contr. Biol. Lab. Sci. Soc. China. Bot. Ser. 12: 121. 1939.

An evergreen shrub or small tree 6–8 m. high, branchlets glabrous, the current year's growth 3–4 mm. in diameter. Leaves coriaceous, lanceolate, 7–13 cm. long, 2–3.5 cm. wide, base cuneate, apex acuminate, the acumen 1–2 cm. long, lateral nerves 15–17 pairs, arcuate, 8–13 mm. apart, obscure above, reticulations of veinlets conspicuous beneath; margin subentire, the apical half remotely sharp-serrate, both surfaces glabrous, the

principal nerves very sparsely pilose beneath; petioles 10–15 mm. long, sparsely pilose. Racemes 2–8, subumbelliform, 8–12 cm. long, densely castaneous-hirsute, the hairs tufted; pedicels 1.5–2 mm. long; sepals ovate, 2 mm. long, obtuse or acute; petals 2.5–3 mm. long, 1.5 mm. wide; filaments glabrous, apex of the anthers divergent; style undivided, 3 mm. long after anthesis, the apex slightly enlarged, lobate. Fruit 3 mm. in diameter.

KWANGSI: *R. C. Ching* 6854, 7209. YUNNAN: *H. T. Tsai* 51447 (type, not seen).

Occurring in woods at altitudes of 1130–1600 m.; a very distinct species, closely related to *C. faberi*, but distinguished by its subentire leaves, very small flowers, short pedicels and its short, persistent style.

POLYPLOIDY IN ENKIANTHUS (ERICACEAE)

HALLY J. SAX

ENKIANTHUS is a comparatively small genus belonging to the Ericaceae. According to Rehder (1940, 1949) there are about ten species, although more than double that number have been reported. Many of the so-called species which were described in isolated instances were considered by Rehder (1940) and Wilson (1907, 1929) to be geographical forms of species already described.

Most species of *Enkianthus* are attractive shrubs or small trees growing wild in southeastern Asia, Japan, southern, central and western China, and the Himalayas. Fang (1935), in a preliminary study of the Chinese species, said that there is not a single species in the northern provinces of China. He commented that only six of the twenty-one species described are valid.

The confusion in the classification of the genus is not surprising. J. D. Hooker (1879) wrote, "The Eastern genus *Enkianthus* presents four types of structure which almost indicate as many genera and would do so if the species had not been united by habit and if the characters were associated instead of applying to one species only."

The number of chromosomes in *Enkianthus* was studied to determine if there was polyploidy in the genus. The variety in the structure of the flowers in the small number of species of *Enkianthus*, as well as their limited distribution, would offer possibilities of interesting combinations. Stomatal size and shape were also determined to learn if there was any correlation between stomatal size and chromosome number in the genus.

Three species of *Enkianthus* with some varieties are growing in the Arnold Arboretum: *E. campanulatus* (Miq.) Nichols, with vars. *albiflorus* Mak. and *palibinii* Bean; *E. perulatus* (Miq.) Schneider; and *E. subsessilis* (Miq.) Mak. Some of these on Bussey Hill were planted as early as 1890. A more recent and successful planting of the same species was made on low ground along the meadow road to the administration building. *Enkianthus cernuus* (Sieb. & Zucc.) Mak. var. *rubens* (Maxim.) Mak. is now being propagated in the Arboretum greenhouse. The chromosome numbers of the species of *Enkianthus* in the Arnold Arboretum were studied from meiotic divisions in the pollen mother cells, from the divisions of somatic cells in the ovary and from regenerating parenchyma of the stem. Very good preparations of divisions in both metaphase and anaphase in the dividing egg cell were also obtained.

The regenerating parenchyma is obtained according to the bark-peel method developed by Sax (1959). A longitudinal section of the bark is removed from the growing stem. The wound is covered with a strip of polyethylene film and left for several days. The newly developed tissue

is then sliced off and fixed. The anthers, ovules and bark tissue were fixed in alcohol-acetic solution for twenty-four hours. The material was then changed to 95 per cent alcohol. Pieces of these tissues were macerated and smeared on a slide and stained with acetocarmine. Camera lucida drawings were made from some of the slides. I wish to thank Dr. Karl Sax for making the bark peels and for checking most of the counts.

The chromosomes were counted in the divisions of the pollen mother cells in *Enkianthus subsessilis* and several plants of *E. campanulatus* including the varieties *albiflorus* and *palibinii*. The chromosomes were also counted in the somatic tissue of the ovules. In the case of *E. perulatus*, counts were made in the somatic tissue in the ovule where it was possible to obtain several very good division figures where the chromosomes could be counted. Counts were also made from the regenerating bark in *E. perulatus* and *E. campanulatus*, where very good preparations of the divisions in the large parenchyma cells were obtained. In all cases several very good preparations were obtained.

Enkianthus subsessilis was found to be a diploid with 11 chromosomes in the meiotic divisions in the pollen mother cells. They were very clear in the preparations and could easily be counted in both the metaphase and anaphase stages. The camera lucida drawings show clearly 11 bivalent chromosomes in the first metaphase of the dividing nucleus of the pollen mother cell (FIG. 1). The 11 anaphase chromosomes are very clear in



FIGS. 1-6. Chromosomes of *Enkianthus*. 1, *E. subsessilis*, first meiotic metaphase; 2, *E. subsessilis*, second meiotic metaphase; 3, *E. perulatus*, somatic metaphase; 4, *E. campanulatus*, first meiotic metaphase; 5, *E. campanulatus*, second meiotic metaphase; 6, *E. campanulatus* var. *albiflorus*, second meiotic metaphase. All figures approximately $\times 1000$.

FIG. 2 just as they are oriented at the poles. There were 22 chromosomes in the somatic tissue of the developing ovule (TABLE I).

Enkianthus perulatus is also a diploid. The count in this case was made in the somatic tissue of the ovule and in the parenchyma of the regenerating bark. Very clear counts in both metaphase and anaphase were obtained. There were 22 chromosomes in the somatic tissue, as is shown in FIG. 3 which was drawn from parenchyma tissue obtained by the bark-peel technique.

Enkianthus campanulatus is a high polyploid — presumably an octoploid — with approximately 88 chromosomes. There were about 44 chromosomes in the divisions of the pollen mother cells of several plants labeled as this species. Multivalent chromosomes were present and an occasional univalent was seen. The divisions were regular, suggesting some degree of allopolyploidy. Only in a few cases were there any lagging chromosomes. Camera lucida drawings were made of the dividing nuclei from several of these plants; all show approximately 44 chromosomes (FIGS. 4, 5).

Enkianthus campanulatus var. *albiflorus* is also an octoploid with $n = 44$ at meiosis. Multivalent associations of three and four chromosomes were seen in some cases, but bivalents predominated. The divisions were regular except in rare instances (FIG. 6). The number of chromosomes in the regenerating bark and in the ovule was over 80, the counts varying from 82 to 89. The chromosomes were small and it was difficult to be exact with such large numbers. TABLE I shows the number in each case.

The two diploid species belong in different sections of the genus, while the octoploid is in a third section. Polyploidy is not necessarily associated

TABLE I. Chromosome Numbers in *Enkianthus*

SPECIES	ARBORETUM NO.	MEIOTIC	SOMATIC	ZONE *
<i>E. campanulatus</i>	14528-1-D	44±	80-87	IV
	14528-1-G	44±		
	14528-1-C		88±	
	23001-1-C		88±	
	7692	44		
	507-58-D		88±	
	507-58-E		78-87	
var. <i>albiflorus</i>	14783-E	44±		IV
	7039-3-A	44±		
	14783-G		88±	
<i>E. perulatus</i>	20153-B		22	V
	10128-B		22	
	3591		22	
<i>E. subsessilis</i>	2449-B	11	22	V
	2449	11		

* A map of the climatic zones is found in Rehder (21). The zones are numbered from the North Pole southward. They are irregular according to the prevailing climate.

with taxonomic diversity. The fact that the octoploid species shows predominantly bivalent chromosomes at meiosis indicates that it is an amphiploid with different genomes.

Chromosome numbers have been reported for many genera of the Ericaceae (Darlington and Janaki-Ammal, 1945). Longley published the chromosome numbers of *Vaccinium*, a polyploid series with the basic number 12. Hagerup (1928) studied several genera: *Calluna vulgaris*, with 16; *Kalmia*, 24 and 48; *Cassiope hypnoides*, 48; *Erica*, 24; *Chimaphila umbellata*, 26; *Ledum*, 26 and 52; *Ramischia*, 38; and *Pyrola*, 46 and 92.

Wanscher (1933) reported 24 chromosomes in *Phyllodoce*; Wulff (1939), 22 chromosomes in *Moneses uniflora*; Maude (1940), 24 in *Daboecia cantabrica*; Newcomer (1941), 24 in *Gaultheria procumbens*; Callan (1941), 36 chromosomes in *Bruckenthalia*, 22, 44, 66 in *Pernettya*, 22, 44, 88 and 26 in *Gaultheria*, 24 in *Pieris*, 48 in *Andromeda*, 24 in *Leucothoe*, 24 in *Erica*, and 26 in *Arbutus*, *Arctostaphylos*, and *Ledum*. Hagerup (1941) counted 60 chromosomes in *Enkianthus campanulatus*, 26 in *Chimaphila*, and 52 in *Ledum*. Baldwin (1942) found 24 chromosomes in *Oxydendrum arboreum*.

Sax (1930) reported the number of chromosomes in *Rhododendron* as 26 for many species and 52 for two higher polyploids, the latter being native to North America. Nakamura (1931) found 26 to be the chromosome number for nine more species of *Rhododendron*. Janaki-Ammal (1950) reported *Rhododendrons* with $4x$, $6x$, $8x$, and $12x$ chromosomes in the high Himalayas in Eastern Asia, polyploidy increasing with altitude. Li (1957) also found 26 chromosomes in all the species of the "luteum" section of the azaleas, excepting the tetraploid *R. calendulaceum* and its hybrids and one triploid.

Thus, with few exceptions (*Calluna vulgaris*), the basic numbers of chromosomes are 11, 12, and 13. Polyploidy is prevalent in many genera, e.g., *Vaccinium*, *Pernettya*, *Gaultheria*, *Pieris*, and *Ledum*. As noted above, Hagerup (1941) reported 60 chromosomes for *Enkianthus campanulatus*, considering it a high polyploid, and suggesting 12 as the basic number both for *Enkianthus* and for the family.

Enkianthus has a very narrow distribution: southeastern Asia, central and western China, and Japan. The polyploid *E. campanulatus* is more widely distributed than the diploids, which have a narrow range and are limited to the warmer parts of China and Japan. Yet, compared with the *Rhododendrons*, which are native to a large part of both hemispheres, the polyploid *E. campanulatus* which extends from northern Japan to southern and central China and to the Himalayas in West China is a naturally limited species. However, when in cultivation it grows very well in the North Temperate Zone in Europe and the United States. The diploid species *E. perulatus* and *E. subsessilis*, as well as *E. cernuus* var. *rubens*, are also able to grow fairly well when introduced as far north as Boston, Massachusetts.

Stomatal size was also studied in three species of *Enkianthus*. The epidermis was peeled from the leaf and mounted on a slide in a drop

of acetocarmine. Camera lucida drawings were made from the mounted epidermis. The diploids *E. perulatus* and *E. subsessilis* showed very little difference in size, but there was some difference in shape. Although no appreciable difference in size was found between the stomata in *E. perulatus* and *E. subsessilis*, there is a striking difference in size between these diploids and the high octoploid *E. campanulatus*. The stomata of *E. campanulatus* are very much larger than those of the diploids, as was noted by comparing the figures in camera lucida drawings of the stomata of these species. There is a very definite correlation between stomatal size and number of chromosomes in the species of *Enkianthus* studied.

Counts were made of the fertile and sterile pollen grains in the different species. Usually the fertility was high, around 85 per cent, but as low as 35 per cent was found. These latter cases were not consistent for any of the species studied and may not be typical, the aberrance having been caused, perhaps, by factors not studied.

SUMMARY

There are 11 meiotic chromosomes in *Enkianthus subsessilis*, 22 somatic chromosomes in *E. perulatus* and *E. subsessilis*. Both are diploid species.

The meiotic chromosomes in *Enkianthus campanulatus* and var. *albiflorus* are 44, and there are about $88 \pm$ chromosomes in the dividing somatic cells. *Enkianthus campanulatus* and its varieties are octoploids.

The stomatal size in *Enkianthus perulatus* and *E. subsessilis*, both diploid species, is about the same. The stomata of the two differ somewhat in shape. The stomata are much larger in *E. campanulatus*, the octoploid, and its varieties than in the diploids, showing a definite correlation between stomatal size and chromosome number.

Although there is some pairing in threes and fours in *Enkianthus campanulatus*, most of the chromosomes are bivalents in the polyploids.

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THE GENERA OF HYDROPHYLLACEAE AND POLEMONIACEAE IN THE SOUTHEASTERN UNITED STATES¹

KENNETH A. WILSON

HYDROPHYLLACEAE R. Brown ex Edwards (WATERLEAF FAMILY)

Annual, biennial or perennial herbs [or rarely shrubs] with alternate or opposite, entire, pinnately or palmately divided leaves. Inflorescences terminal, axillary, or opposite the leaves, the flowers in cymes, panicles, or solitary. Flowers bisexual, regular, 5-merous. Calyx 5-parted, the sinuses sometimes bearing appendages. Corolla rotate, campanulate or funnellform, 5-parted. Stamens 5, epipetalous. Gynoecium syncarpous; styles 2 (rarely more) or 1, terminal; ovary superior, 1-locular with 2 parietal placentae or 2-locular and the placentation axile. Ovules 4—many, anatropous or amphitropous. Fruit a capsule.

A family of about 18 genera and 250 species in three tribes, primarily of North America, but extending into South America, Asia, and Africa. The family is represented in the United States by 15 genera centered in the Southwest; six genera occur in our area.

The family is regarded as being closely allied to the Polemoniaceae and the Boraginaceae. It may be distinguished from them by the combination of bicarpellary 1- or 2-locular ovary (usually with numerous ovules) and the usually imbricate aestivation of the flowers which are generally borne on scorpioid cymes. Considerable variation is evident in the structure and nature of the ovary. The gynoecium is 2-carpellate; the placentae may be parietal and fleshy or they may be narrow, extending into the ovary to meet without fusing and partition the ovary into two locules. In *Hydrolea* further elaboration of the placentae, accompanied by a fusion of the dividing wall, has produced a 2-locular ovary with axile placentation.

The Hydrophyllaceae are cytologically perhaps the best known family of any size. Information on the chromosome numbers of the species in

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the family has been accumulating, and, along with morphological studies, has already contributed to the understanding of the group. Cytological information, for instance, supports the recognition of subg. *Cosmanthus* of *Phacelia*, and also points to the relationship of *Lemmonia* to *Nama*. A comprehensive knowledge of the cytology of the members of this family will give a clearer indication of the value of chromosomal data in systematic studies. Presently the chromosomes of about 67 per cent of the species (about 200) have been counted, and counts are available for at least one species in each of the described genera.

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KEY TO THE GENERA OF HYDROPHYLLACEAE

- A. Leaves dissected, lobed or toothed; style 1, entire or 2-cleft.
 B. Placentae parietal, dilated, ovary 1-locular.
 C. Flowers in scorpioid cymes; stamens exserted; leaves mostly basal and alternate; seeds not cucullate; plants biennial or perennial. 1. *Hydrophyllum*.
 C. Flowers solitary opposite the leaves or terminal in a loose cyme; stamens included; leaves mostly cauline, all alternate or the lower opposite and the upper alternate; plants annual.
 D. Calyx sinuses auriculate; seeds cucullate; leaves all alternate. 2. *Nemophila*.
 D. Calyx sinuses without auricles; seeds not cucullate; leaves opposite below, alternate above. 3. *Ellisia*.
 B. Placentae parietal, narrow, projecting into ovary and partitioning it into 2 locules but not fusing; flowers in scorpioid cymes; calyx sinuses without auricles; seeds not cucullate; leaves alternate. 4. *Phacelia*.
 A. Leaves entire, simple; styles 2 (rarely 3-5).
 E. Flowers axillary, solitary or paired; placentae parietal, narrow, projecting into ovary and partitioning it into 2 locules but not fusing. 5. *Nama*.
 E. Flowers in cymose inflorescences; ovary 2-locular; placentae axile. 6. *Hydrolea*.

Tribe HYDROPHYLLAE A. Gray

1. *Hydrophyllum* Linnaeus, Sp. Pl. 1: 146. 1753; Gen. Pl. ed. 5. 72. 1754.

Erect, perennial or biennial herbs with membranaceous, pinnate or pinnatifid basal leaves and alternate cauline leaves similar to the basal ones or orbicular to reniform, palmately lobed or divided. Inflorescences simple or branched cymes, terminal. Calyx campanulate, 5-lobed, at times the sinuses with a small appendage. Corolla campanulate, 5-parted, greenish-white or white to purple or violet, with a pair of elongated scales adnate to the corolla tube at the base of each filament. Stamens 5, exserted, the filaments more or less villous; pollen smooth, tricolpate. Style solitary, once branched at the apex, the stigmas capitate; ovary 1-locular with 2 parietal placentae. Fruit a globose, 1-3-seeded capsule. Seeds reticulate, without cucullus. (Including *Decemium* Raf.) TYPE SPECIES: *H. virginianum* L. (Name from Greek, *hydor*, water, and *phyllon*, leaf, in reference to the succulent stems and petioles of *H. virginianum*.) — WATERLEAF.

A genus of eight species in two sections with four species in eastern and four in western North America. All four of the eastern American species occur in our area, all in rich, moist woods. The species of *Hydrophyllum* are very similar in floral and fruit characters, but are distinguishable in the characters of the leaf and of pubescence.

Section HYDROPHYLLUM (perennial and rhizomatous, calyx rarely appendaged) includes seven species, four restricted to western North America, and three in our area. *Hydrophyllum virginianum* ($2n = 18$) ranges from Quebec west to eastern North and South Dakota and south to Maryland, Virginia, Tennessee, Arkansas, and Kansas. Deep-violet-flowered plants from the mountains of West Virginia, Virginia, and North Carolina have been described as *H. virginianum* var. *atranthum* (E. J. Alex.) Constance. Additional field study is needed to determine whether this is merely a color-form occurring among other forms (white to purple) or whether it is in fact the only representative of the species in its area and restricted in its distribution. *Hydrophyllum macrophyllum* Nutt. ranges from western Virginia and West Virginia, west to Illinois, and south to Georgia, Alabama, and Arkansas; and *H. canadense* L. ($2n = 18$) occurs from Massachusetts and Vermont to Ontario and Illinois south to northern Alabama and eastern Missouri.

Section DECEMIUM (Raf.) Gray (biennial with taproot, calyx always appendaged) includes only *Hydrophyllum appendiculatum* Michx. ($2n = 18$) which is distributed from Ontario to Minnesota, south to Pennsylvania, Tennessee, Missouri, and eastern Kansas. The presence of appendages in the sinuses of the calyx lobes and the biennial habit have served as characters in the recognition of the monotypic genus *Decemium* Raf. However, since appendages may occasionally be found in *H. canadense*

and other distinguishing features are only minor floral variations, *Decemium* is to be retained in *Hydrophyllum* which it closely resembles in all other respects.

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2. *Nemophila* Nuttall in Barton, Fl. N. Am. 2: 71. 1822; Nuttall, Jour. Acad. Nat. Sci. Phila. 2: 179. 1822, nom. cons.

Weak, annual herbs with alternate [or opposite, or the lower opposite and the upper alternate] oblong to orbicular, pinnate, pinnatifid or lobed leaves. Flowers solitary on peduncles opposite the leaves or in terminal cymes. Calyx campanulate, deeply 5-parted, the sinuses auriculate [or exauriculate.] Corolla campanulate to rotate, 5-lobed, white or blue, with a pair of scales adnate to corolla lobes at the base of each filament. Stamens 5, included; pollen smooth, tricolpate. Style solitary, shallowly or deeply cleft; ovary 1-locular with 2 parietal placentae. Fruit an ovoid or globose, 1-4[-20]-seeded loculicidal capsule. Seeds cucullate, regularly [or irregularly] pitted [or without evident pits]. (*Viticella* Mitch., nom. rejic.; *Galax* L. 1753 [partim], 1754, nom. rejic.) TYPE SPECIES: *N. phacelioides* Nutt. in Barton. (Name from Greek, *nemos*, a grove, and *philein*, to love, in reference to the habitat of *N. phacelioides*.)

A genus of eleven species with nine in western North America and two in the southeastern United States. The species are distinguished on the basis of leaf shape and arrangement, nature of the seeds, color and shape of the corolla, nature of the auricles, and pubescence of the stems and leaves. A number of growth forms of various species have been described and named, mostly as a result of misinterpretation of the behavior of the species during the growing season. As the season progresses, most species pass from a small, erect, and unbranched stage to an elongated, decumbent, and branched one. The flowers also often become smaller and altered in their shape.

Our two species occur in moist and shaded woods. *Nemophila phacelioides* Nutt. ($2n = 14$) (corollas blue or purplish, 1-3 cm. broad, auricles prominent) ranges from southern Texas and Louisiana north to Arkansas and Oklahoma. It is cytologically unique in its seven pairs of chromosomes which are nearly twice as large as the nine pairs of the ten other species. *Nemophila microcalyx* (Nutt.) Fisch. & Mey. (corollas white, 0.5 cm. or less broad, auricles minute) ($2n = 18$) ranges from southeastern Texas north to Arkansas, and southeastern Missouri, east and north to Florida, Tennessee and Virginia.

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3. *Ellisia* Linnaeus, Sp. Pl. ed. 2. 2: 1662. 1763, nom. cons.

Simple or diffusely branched, weak annual herbs with oblong to ovate or deltoid-ovate, pinnately divided leaves, the lower opposite and the upper alternate. Flowers solitary on peduncles opposite the leaves or in terminal cymes. Calyx campanulate, deeply 5-parted, auricles none. Corolla narrowly campanulate, 5-lobed, white or bluish, with a pair of minute scales adnate to each corolla lobe at the base of each stamen. Stamens 5, included; pollen smooth, tricolpate. Style solitary, 2-cleft; ovary 1-locular with 2 parietal placentae. Fruit a globose, usually 4-seeded capsule. Seeds without a cucullus, regularly reticulate. $2n = 20$. (*Macrocalyx* Ehret ex Trew, Nova Acta Acad. Leop.-Carol., nom rejic.; *Nyctelea* Scopoli.) TYPE AND SOLE SPECIES: *E. Nyctelea* (L.) L. (Named in honor of the English naturalist John Ellis, 1710-1776.)

A monotypic genus with disrupted distribution, occurring in rich woods and on stream banks from New Jersey and Pennsylvania to North Carolina (?) and on the prairies and plains of Manitoba to Alberta, southeast and south to Indiana, Illinois, Arkansas, Oklahoma, and New Mexico. It is also known as an adventive in disturbed areas in the northeastern United States.

Ellisia resembles *Pholistoma* and *Nemophila*, but is distinguished by its seeds which lack a cucullus, its unarmed capsules, and its hispid or glabrate stems. Although closely related to these groups, *Ellisia* is believed to be a distinct and natural genus.

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Tribe PHACELIEAE A. Gray

4. *Phacelia* Jussieu, Gen. Pl. 129. 1789.

Annual, biennial [or perennial] herbs with alternate, lobed or pinately divided leaves. Inflorescences scorpioid cymes. Calyx deeply 5-parted. Corollas rotate to campanulate, 5-lobed, white to lavender or bluish violet, without scales, a gland bearing two parallel flaps adnate to the corolla tube between each pair of stamens. Stamens 5, exerted or included. Style 2-cleft; ovary with two 2–14-ovuled parietal placentae which meet and partition the ovary into 2 locules. Fruit an ovoid 4-many-seeded capsule. Seeds finely reticulate to alveolate or rugose. TYPE SPECIES: *P. secunda* J. F. Gmelin (*P. magellanica* (Lam.) Coville). (Name from Greek, *phacelos*, a fascicle, in reference to the cymose inflorescences.) — SCORPION WEED.

A genus of perhaps 100 species of temperate North and South America. placed by Brand in six sections. All of our species belong to subg. *Cosmanthus* (Nolte ex A. DC.) Constance (sect. *Cosmanthus* Nolte ex A. DC.). The genus itself is characterized by the scorpioid cymes and by the narrow placentae which project into the ovary and meet, thereby producing two locules.

Subgenus *COSMANTHUS*, with 14 species, occurs from the highlands of Guatemala and Mexico, north into Texas, east to Georgia and North Carolina, and north to Oklahoma, Missouri, Illinois, Ohio, Pennsylvania and New York, primarily in rich woods, clearings, and fields. Ten species and varieties occur in our area. All of our species are annuals, except *Phacelia bipinnatifida* Michx. (including *P. brevistyla* Buckl.) ($2n = 18$), a biennial distributed from West Virginia to Georgia and Alabama, west to Illinois, Missouri, and northeastern Arkansas. This species, formerly placed in sect. *PHACELIA* because of its prominent glands and their associated scales, belongs properly in subg. *COSMANTHUS* on the basis of its other morphological features and its distribution.

Phacelia Purshii Buckl. (including *P. Boykinii* (A. Gray) Small and *P. Bicknellii* Small) ($2n = 18$) is widely distributed in eastern North America. Both large-flowered plants of *P. Purshii* and similar small-flowered plants (*P. Bicknellii* ?) grow together in the vicinity of Nashville, Tennessee, suggesting the need for additional investigation. *Phacelia dubia* (L.) Trel. var. *dubia* ($2n = 10$) is also of wide distribution in eastern North America, while *P. dubia* var. *georgiana* McVaugh is an endemic of the granite flat rocks of Georgia and Alabama.

Phacelia strictiflora (Engelm. & Gray) Gray var. *Robinsii* Constance ($2n = 18$), of Alabama, Missouri, Oklahoma, and Texas, has characters intermediate between *P. strictiflora* var. *Lundelliana* Constance ($2n = 18$) (Texas and Oklahoma) and *P. hirsuta* Nutt. ($2n = 18$) (Missouri, Kansas, Arkansas, Louisiana, Oklahoma, Texas) and is suspected of having arisen through the hybridization of those two taxa. Similarly,

hybridization of *Phacelia hirsuta* and *P. Purshii* appears to have given rise to *P. gilioides* Brand ($2n = 18$) (Missouri, Kansas, Oklahoma).

Our other species are *Phacelia ranunculacea* (Nutt.) Constance (*P. Covillei* S. Wats.) ($2n = 28$), peculiar in its tubular-campanulate corolla, vestigial glands, semiglobose seeds, chromosome number, and disrupted distribution (Maryland, District of Columbia, Virginia and Indiana, Missouri, Tennessee, North Carolina, Arkansas); *P. maculata* Wood ($2n = 10$), from the southern Appalachians; *P. glabra* Nutt. ($2n = 16$), unique in its chromosome number; and *P. fimbriata* Michx. ($2n = 18$). In spite of the different chromosome numbers among the species in subg. *COSMANTHUS*, the absence of the number 11, which is common among the other members of the genus, supports the distinctness of the group. It is also the only group of *Phacelia* in which there is a 9-paired perennial species (*P. platycarpa* (Cav.) Spreng.).

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5. **Nama** Linnaeus, Syst. Nat. ed. 10. 2: 950. 1759, partim, emend. Choisy in DC. Prodr. 10: 182. 1846, nom. cons.

Prostrate or ascending, annual [or perennial] herbs with alternate [rarely opposite] entire leaves. Flowers solitary or paired in the axils of leaves [or in reduced lateral or terminal cymes]. Calyx deeply 5-parted, accrescent. Corolla tubular, 5-lobed, purple or white. Stamens 5, included, unequally inserted on the corolla tube, the filament bases usually dilated, the adnate portion with [or without] free margins. Styles 2, free, or at times united about half their length [or completely united]; ovary multiovulate, appearing 2-locular as a result of the intrusion of the 2 parietal placentae. Fruit a loculicidal [or either loculicidal or septicidal] many-seeded capsule. Seeds variously pitted, alveolate [or reticulate to smooth]. (*Nama* L., 1753, *Conanthus* S. Wats., *Marilau-nidium* O. Ktze., nomina rejicienda; not *Nama* sensu Small = *Hydrolea* L.) TYPE SPECIES: *N. jamaicensis* L. (Name from Greek, *nama*, a river or stream, in reference to the habitat of *Nama zeylanica* L. [= *Hydrolea zeylanica* (L.) Vahl.] the only species mentioned by Linnaeus in 1753.)

A genus of about 35 species in five sections, primarily of Mexico and the southwestern United States, but also in South and Central America, the West Indies, and (one species) the Hawaiian Islands. In our area the genus is represented only by *Nama jamaicensis* L. ($2n = 28$), of sect. NAMA (leaves entire, styles free or only partially united, capsules membranous), which occurs in hammocks, roadsides, and disturbed areas, and ranges from El Salvador and the West Indies, north to Texas, Florida, and Louisiana.

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Tribe HYDROLEAE Choisy

6. *Hydrolea* Linnaeus, Sp. Pl. ed. 2. 1: 328. 1762, nom. cons.

Annual or perennial herbs with alternate, simple leaves. Inflorescences axillary or terminal cymes. Calyx deeply 5-parted. Corolla rotate to campanulate, 5-parted, blue, rarely white, without scales. Stamens 5, exerted or included, the filament bases dilated, inserted on corolla tube. Styles 2, rarely 3–5; ovary 2-locular, multiovulate, placentation axile, the placentae 2-branched [or entire]. Fruit a 2–4-valved, or irregularly dehiscent capsule. Seeds longitudinally ribbed. (*Nama* L., 1753, not 1759, nom. rejic.) TYPE SPECIES: *H. spinosa* L. (Name from Greek, *hydor*, water, apparently in reference to the aquatic habitat.)

A genus of about 19 species (in two sections) in aquatic habitats in the tropics of the world. Section ATTALERIA Brand (placentae entire) with about five species, is entirely Old World (occurring primarily in Africa and Asia). Section HYDROLEA (sect. *Sagnonea* (Aubl.) Brand) (placentae divided into two parts) is limited to the Americas and contains about 14 species ranging from Paraguay and Uruguay, to Brazil, north to Mexico, the West Indies, and the eastern United States.

Hydrolea uniflora Raf. (*H. affinis* Gray) (Texas to Mississippi and northern Florida, north to Oklahoma, southern Missouri, southern Indiana, and southern Illinois) has glabrous stems and lance-ovate calyx lobes which equal the corolla in length. *Hydrolea quadrivalvis* Walt. ($2n = 20$) (northern Florida to Louisiana, north to southeastern Virginia) has stems which are villous-hispid, and linear or linear-lanceolate calyx lobes which equal the corolla. These two species seem to be very closely related and differ mainly in the pubescence of the stem. Field observations and collections of the two, particularly in the area where they overlap, should be valuable in clarifying their relationship. Our other two species are *H. ovata* Nutt. (Texas to Georgia, north to Missouri) with ovate leaves, pubescent stems and calyx segments shorter than the corolla, and *H. corymbosa* Macbride ex Elliott (southern Florida to Georgia and South Carolina) with elliptic to elliptic-lanceolate leaves, glabrate stems, and calyx segments shorter than the corolla.

Hydrolea spinosa L., of the American tropics, has also been reported to have 20 pairs of chromosomes.

POLEMONIACEAE Jussieu (PHLOX FAMILY)

Annual, biennial, or perennial herbs [shrubs, vines, or small trees], with opposite or alternate, simple or pinnately [or palmately] dissected leaves. Inflorescences cymose or flowers rarely solitary. Flowers bisexual. Calyx 5-parted. Corolla 5-parted, salverform to rotate, the aestivation contorted. Stamens 5, alternate with the corolla lobes, equally or unequally inserted on the corolla, the anthers introrse. Gynoecium syncar-

pous, stigmas 3[rarely 2]-lobed, style 1, ovary superior, 3[rarely 2]-locular, each locule with 1-many anatropous ovules, the placentation axile. Fruit a loculicidal capsule [rarely indehiscent]. Seeds with a straight embryo and abundant endosperm. TYPE GENUS: *Polemonium* L.

A family of about 300 species variously interpreted to represent about 12 to 23 genera placed in four tribes and two subfamilies by Brand, and in five tribes by Grant. The tribes COBAEAE Baill., CANTUEAE Peter and BONPLANDIEAE Baill. contain tropical genera of shrubs, vines or small trees (*Cobaea* Cav., *Cantua* Juss., *Huthia* Brand, *Bonplandia* Cav. and *Loeselia* L.) and range from Mexico south to Chile. The temperate, primarily herbaceous, genera fall in tribe POLEMONIEAE Baill., which includes the well-marked genera *Phlox* and *Polemonium*, and in the tribe GILIEAE Reichb., which includes *Gilia*, a genus which has been considered by some authors to include almost all of the remaining species in the subfamily, a complex of polymorphic species which is poorly understood. The Polemoniaceae are centered primarily in western North America, but extend south into Mexico, Peru, and southern Chile, east to eastern North America, and also into Asia and Europe. In our area the family is represented by *Phlox*, *Polemonium*, and *Ipomopsis*. The weedy *Colomia linearis* Nutt. ($2n = 16$) is known in Missouri and may perhaps also become established within our region.

The family has been a perplexing problem with respect to its phylogenetic relationships. It has been considered to be derived from a sympetalous relative of the Rosales, from the Geraniales, and from the Primulales. The Polemoniaceae seem to be allied to the Convolvulaceae, which they resemble in their inflorescences, corolla, stamens, and anatropous ovules. However, on the basis of a morphological study of the flowers, Dawson concluded that they are closely related to the Caryophyllaceae and Geraniaceae, and interpreted the family as representing an evolutionary line from a 3-carpellate caryophyllaceous stock which arose prior to the establishment of the free-central placentation of the Caryophyllaceae. *Cantua* and *Cobaea* were interpreted as primitive genera: they differ from other Polemoniaceae in their woody habit and in having two whorls of stamen traces. Cytologically, the subfamily COBAEOIDEAE differs in having a larger number of chromosomes which have a much smaller size than those of the genera of the POLEMONIOIDEAE.

The family is particularly popular in horticulture, and almost all of the genera are known in cultivation.

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KEY TO THE GENERA OF POLEMONIACEAE

- A. Leaves simple, opposite; perennials or annuals; stamens unequally inserted on the corolla tube. 1. *Phlox*.
- A. Leaves pinnately divided, alternate; stamens equally inserted on the corolla tube.
- B. Leaves once pinnately divided, the leaflets oval to lanceolate; flowers blue or white; perennial. 2. *Polemonium*.
- B. Leaves deeply pinnately dissected into narrow, linear lobes; flowers red, pink, or white; biennial. 3. *Ipomopsis*.

Tribe POLEMONIEAE Baill.

1. *Phlox* Linnaeus, Sp. Pl. 1: 151. 1753; Gen. Pl. ed. 5. 75. 1754.

Perennial or annual, herbaceous or more or less woody, erect, decumbent or trailing plants with opposite, alternate or subopposite sessile or petioled leaves. Inflorescences cymose, terminal or in the axils of the uppermost leaves. Calyx tubular, angled, 5-parted, not accrescent, rupturing as the capsule expands. Corolla salverform, 5-parted, purple, to lavender, to pink to white. Stamens 5, unequally inserted on the corolla tube, exserted or included. Style 1; stigmas 3; ovary 3-locular, each locule with 1-3 anatropous ovules. Fruit a loculicidal capsule. TYPE SPECIES: *P. glaberrima* L. (Name from Greek, *phlox*, flame, the ancient name for *Lychnis*, transferred to this genus.)

A genus of about 67 species primarily of North America, ranging from northern Mexico to the United States and southern Canada, and in Alaska to adjacent Yukon and Northwest Territories; a single species in northeastern Asia (Siberia). In our area the genus is represented by about seventeen species, most of which are known also in cultivation.

The genus has been variously subdivided into six sections by Peter; two subgenera, five sections and two subsections by Brand; and into three sections and eighteen subsections by Wherry. The major subgeneric divisions are based on such characters as the habit of the plant, the length of the style, the size of the seed and embryo, and the length of the stamens. Additional divisions are based on the shape of the corolla, minor leaf variations, as well as leaf arrangement, and pubescence. It seems questionable that the numerous subdivisions of the genus are natural and that all are worthy of taxonomic recognition. It is probable that a genetic study of the genus would help to clarify problems of interrelationships of the species which are not apparent on the basis of morphological studies alone.

The variation within the species of *Phlox* has often led to widely different taxonomic treatments. The variation in a population of *Phlox bifida* Beck from Tennessee has been interpreted as the result of introgressive hybridization with *P. amoena* Sims. Further studies of this kind are needed to help explain the nature of the variation in different species. *Phlox Drummondii* Hook., an annual native to Texas, is widely grown as an ornamental and has become naturalized as far east as Georgia and Florida. Hundreds of forms of *P. Drummondii*, differing in flower color, shape of the corolla, and pubescence have arisen in cultivation, and the remarkable variation in the species has been the subject of numerous studies. At least some of the corolla variations seem to be related to single genes.

Most of the species which have been examined cytologically are diploids ($2n = 14$). Both diploid and tetraploid ($2n = 14, 28$) plants have been reported in *Phlox Drummondii*, as well as in *P. subulata* L. A triploid known in cultivation may possibly represent a hybrid of *P. maculata* L. and *P. carolina* L., although tetraploids are not known in either of the supposed parental species. Short- and long-styled species of *Phlox* occur, but whether style-length serves as a barrier to fertilization, as has been suggested in *Polemonium*, is not known.

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2. *Polemonium* Linnaeus, Sp. Pl. 1: 162. 1753; Gen. Pl. ed. 5. 76. 1754.

Perennial [or annual], erect or decumbent herbs with alternate, pinnately divided leaves. Inflorescences cymose, terminal or axillary. Calyx campanulate, herbaceous, accrescent. Corolla campanulate to funnel-form, 5-parted, blue or white, [yellow, pink, or purple]. Stamens 5, equally inserted on the corolla tube, included [or exserted]. Style 1; stigmas 3; ovary 3-locular, each locule with 1–10 ovules. Fruit a loculicidal capsule. TYPE SPECIES: *P. caeruleum* L. (Derivation of name uncertain; perhaps from Greek, *polemos*, war, or perhaps named for *Polemon*, an early Greek philosopher.) — JACOB'S LADDER, GREEK VALERIAN.

About 20 species, primarily of western North America, ranging from the mountains of Mexico north to Alaska and northern Canada, extending into eastern North America, and also into Asia and Europe; a single species in southern South America. Represented in our area by only one species, *Polemonium reptans* L., of rich woods and damp meadows from Wisconsin to New Hampshire, south to Oklahoma, Arkansas, Mississippi, Alabama, Georgia, and North Carolina.

The variation of most of the species of *Polemonium* has not been studied in great detail and, consequently, considerable confusion exists in the understanding of the species and their interrelationships. *Polemonium reptans* varies in its size, in the shape and number of the leaflets, in the shape of the sepals and in the degree and nature of pubescence. Varietas *villosum* E. L. Br. was described from Ohio and Kentucky and is characterized by its densely glandular-villous inflorescence. The correlation of the restricted distribution of var. *villosum* with the disjunct occurrence of other species which have been considered to have a relic distribution has led to the interpretation that its present range is a remnant of an earlier, more extensive one. The pubescence of some plants of the widespread *P. reptans* var. *reptans* in Ohio, and also in Pennsylvania, is considered to show evidence of introgression with var. *villosum*. Further studies of the variation of *P. reptans* in other areas should contribute more information on the validity of this hypothesis.

The species which have been examined cytologically have a chromosome number of $2n = 18$; polyploidy has been reported in *Polemonium californicum* Eastwood ($2n = 36$) and in *P. caeruleum* L. subsp. *Van-Bruntiae* (Britt.) Davidson (*P. Van-Bruntiae* Britt.) ($2n = 36$), of Maryland and West Virginia and north to Vermont.

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3. *Ipomopsis* Michaux, Fl. Bor.-Am. 1: 141. 1803.

Biennial [perennial, or annual] herbs with alternate pinnatifid leaves, the tips of the leaf segments bearing a horny mucro. Inflorescences cymose, each flower subtended by a bract. Calyx herbaceous, 5-parted, not accrescent, rupturing as the capsule expands. Corolla salverform or funnellform, 5-parted, red, pink, white [violet or yellow]. Stamens 5, equally inserted on the corolla tube or in the sinuses of the corolla, included or exserted. Style 1; stigmas 3; ovary 3-locular, each locule with 1-many ovules. Fruit a loculicidal capsule. TYPE SPECIES: *I. elegans* Michx. (= *I. rubra* (L.) Wherry). (Name from *Ipomoea* and Greek, *opsis*, aspect, in reference to the similarity of the corolla to that of species of *Ipomoea* of sect. *Quamoclit* Meissn.)

A genus of about 20 or more species in three sections, centered primarily in the Rocky Mountains and the adjacent plains, but extending west to the Pacific coast and east to the Carolinas and Florida, south to Texas and Mexico; one species in Argentina and Chile. A single species in our area, the biennial *Ipomopsis rubra* (L.) Wherry ($2n = 14$), occurring in sandy soil in fields and roadsides from Texas to Oklahoma, east to North Carolina and Florida, also escaped from cultivation and naturalized as far north as Illinois, Michigan, and Massachusetts.

A segregate of the heterogeneous genus *Gilia* R. & P., *Ipomopsis* appears, on the basis of the presently available information, to form a natural group. It is distinguished by the primarily perennial or biennial habit of the species, the leafy stems, pinnately dissected leaves, bracteate flowers, salverform or funnelform corollas (without an evident throat), waxy, curved seeds, and seven pairs of large chromosomes (insofar as studied). Further studies on the cytology, genetics, morphology and ecology of the members of this group are needed in order to establish more clearly the validity of the genus as a segregate of *Gilia*. In a discussion of the genus, Grant remarked that "*Ipomopsis* seems to be as distinct from *Gilia* as is *Eriastrum* or *Langloisia* or *Navarretia*. If the system of classification is to be internally consistent, therefore, the only alternative to recognizing *Ipomopsis* as a genus is to treat it and *Eriastrum*, *Linanthus*, etc., as subgenera of *Gilia*. Phylogenetically it does not matter whether we recognize a tribe *Gilieae* composed of the genera *Gilia*, *Ipomopsis*, *Eriastrum*, *Linanthus*, etc., or one inclusive genus with subgenera."

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STUDIES IN THE GENUS COCCOLOBA, IX.
A CRITIQUE OF THE SOUTH AMERICAN SPECIES

RICHARD A. HOWARD

THE FIRST SIX PAPERS of this series treated the West Indian species of the polygonaceous genus *Coccoloba*, with the work based largely upon field studies in this area. The seventh paper dealt with the species of Central America and Mexico; the writer has only a slight knowledge of these species in the field, but fortunately had available an unusually large number of collections as well as extensive field notes made by recent collectors. This paper will treat the species of South America. The limitations of this study are greater both from lack of field knowledge and the fewer specimens available. For these reasons, this treatment is probably more conservative than future workers will deem necessary. The goals of this study have been 1) to bring together all records of taxa of *Coccoloba* for South America; 2) to correct existing errors of literature citation; 3) to evaluate and compare published species where possible; 4) to locate the existing type collections; and 5) to select lectotypes of many species. It is hoped that these notes will encourage collectors and botanists in the area to gather complete material of the species and to record adequately the variations so as to allow a better understanding of certain morphological problems. Only then can the monographer prepare complete descriptions and keys for the species in South America.

The earliest comprehensive treatment of the species of *Coccoloba* in South America was prepared by Meisner for the *Flora Brasiliensis* (5(1): 23-44. 1855). Although some species were illustrated, the descriptions in general were inadequate and no keys were given. Specimens cited previously from the Martius herbarium have since been found in Brussels, Munich, and Leningrad, and a few numbers have been widely scattered. Representative specimens of several species attributed to Martius could not be located for this study and in some other species the selection of a lectotype has required very careful comparisons between specimens from several herbaria and published descriptions.

In 1856 Meisner provided a synopsis of the genus for DeCandolle's *Prodromus* (14: 150-171). One might expect that many of the specimens which Meisner cited would be in the *Prodromus* herbarium or in the Delessert herbarium at Geneva, but, unfortunately, very few are represented in either collection. Meisner's personal herbarium, which has been acquired by the New York Botanical Garden, includes specimens of most species of *Coccoloba*. A few of these are small fragments, yet they represent the only existing type material for certain species.

The only complete monograph of *Coccoloba* was prepared by Lindau

and published in 1890 in Engler's *Botanischer Jahrbücher* (13: 106-229). Many adjustments are necessary therefore to bring the specific names into conformity with the present rules of nomenclature. Lindau's descriptions are not models of accuracy, and the key published in the monograph contains so many errors of fact that it is almost unusable. Following the description of a plant, Lindau cited the collector's name and collection number and at the end gave a list of the herbaria in which he had seen the material. In the selection of a lectotype, therefore, it has been necessary to associate the collection with a particular herbarium. The information supplied in this paper should make easier the work of the next monographer who wishes to obtain material for study.

Lindau frequently cited specimens to be found only in the Berlin herbarium. A study of these, annotated by Lindau, has shown them to be fragments of specimens from other herbaria. There is a question whether the holotype is really the Berlin fragment and only specimen the author cited, or the more ample specimen in some distant herbarium which the author may not have seen and did not annotate.

The specimens of *Coccoloba* in the Vienna herbarium were lost or destroyed during World War II. According to Lindau's citations some of the Jacquin material was at Vienna and is no longer available. A very few of the Vienna specimens were photographed before 1940, and prints of these in the herbarium of the Chicago Natural History Museum are the basis for discussion of these names here.

Most existing treatments of the genus have assumed the flowers to be perfect. During field study of the species in the West Indies the author determined that the flowers are functionally unisexual and that the plants are dioecious. Recently Buchinger and Sanchez examined the species found in Argentina and concluded (Bol. Soc. Argent. Bot. 7: 251-255. 1959) that one species of *Coccoloba* in that country is truly dioecious, but that the remainder have perfect flowers or are monoecious. Very few collections are cited in their work and none of those was available to me. I have examined many specimens which I assign to these same species from Argentina and find no evidence in the herbarium specimens to support their conclusions. In the specimens which I examined the flowers with conspicuous pistils have small or rudimentary stamens which do not produce pollen. Flowers with large stamens which produce pollen appear to have undeveloped or rudimentary pistils. There were no specimens with pollen-producing flowers and fruits on the same branches. I do not doubt their decision, since it was based on field study of carefully selected material, but I do point out the difficulty of stating definitely the sexual condition in herbarium specimens and the futility of using in a key such contrasting characteristics as plants monoecious or plants dioecious.

The species in the West Indies were studied in the field to determine leaf variation. I found that vigorous terminal shoots, short branches, branches of average growth, and adventitious shoots might all have different sizes and shapes of leaves. This leads one to question Lindau's

descriptions and keys, since he seems to have relied much on the size and shape of leaves and particularly on the shape of the leaf base.

The habit of the plant also was found to be variable in West Indian species. Some are shrubby or tree-like at the base, but with scrambling branches having the appearance of lianas. Thus herbarium specimens consisting of flowering or fruiting branches without adequate habit notes may not be indicative of the true character of the species.

Relatively few of the South American species considered in the following notes are represented by both flowers and fruit. In some cases it has been possible to associate as one taxon certain flowering and fruiting specimens originally described as separate species. When peculiarities of growth can be properly associated with flowering and fruiting specimens additional species will undoubtedly be combined. Throughout the following text I have been conservative in maintaining as distinct species all specimens concerning which there may be some question. When further evidence becomes available, many of these species may be united.

I have been fortunate to have on loan for study the important historical collections of *Coccoloba* from the Botanisches Museum, Berlin, which formed the basis for Lindau's work; the Jardin Botanique de l'État, Brussels, which include many Martius collections; the Botanische Staatssammlung, Munich, also rich in Martius material; the New York Botanical Garden which include recent collections, as well as Meisner's personal herbarium; and the Herbarium of the Department of Systematics and Plant Geography of the Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad, which contains so many duplicates of classic collections. I am most grateful to the directors and curators of these institutions for making their collections available for an unusually long period of time. Selected collections have been borrowed from other institutions and I have visited still more herbaria for study. The many courtesies which made this publication possible are much appreciated. The standard abbreviations of Index Herbariorum have been used in this paper.

Species of *Coccoloba* have been reported from every country in South America, with the sole exception of Chile. In the citation of specimens the countries and their subdivisions, as well as the specific localities of collections, are listed in alphabetical order.

Coccoloba acrostichoides Chamisso, *Linnaea* 8: 132-133. 1833; Meisner, *Fl. Bras.* 5(1): 33. *pl.* 13, *fig.* 2. 1855; Lindau, *Bot. Jahrb.* 13: 138. 1890.

Coccoloba rubiginosa Martius ex Meisner, *Fl. Bras.* 5(1): 33. 1855, in syn.

Chamisso did not cite a specimen in the original description, and previous monographers have not indicated a type. There is a specimen in the Leningrad herbarium collected by Sellow and bearing on the label the name "*Coccoloba acrostichoides* N" and the annotation "Hb. Cham." This specimen is probably authentic. A more ample specimen in the Berlin herbarium has a tag which bears the number "1393" attached but lacks

the reference to the Chamisso herbarium. Lindau did not see or cite either of these collections, yet one must be considered the lectotype and I so designate the specimen at Berlin. All other Sellow collections, including those cited by Lindau, are annotated "*Coccoloba acrostichoides* Cham. et Schl."

The illustration in *Flora Brasiliensis* well represents this species. A printer's proof of this drawing is in the Brussels herbarium and the specimen *Claussen* 330 is mounted on the same sheet. There is little similarity between the two, and the illustration appears to be a compilation.

Coccoloba acrostichoides is one of the most distinctive species of the genus, with copious dark-brown pubescence on the lower leaf surface. In leaf shape and in the nature of the inflorescence it is similar to *C. brasiliensis*. The species is not known in fruit and I have not seen any collections more recent than those of Glaziou.

Coccoloba rubiginosa Martius ex Meisner was published in synonymy and has no validity. A specimen at Munich from the Martius herbarium bears this name, but no location or collector is indicated.

Brazil. MINAS GERAIS: Ouro Preto, *Glaziou* 15356 (BR, LE); without specific location, *Claussen* 330 (BR). RIO DE JANEIRO: San Antonio, *Sellow* "B 1393. c 429" (B). LOCATION NOT KNOWN: Herb. *Martius* s.n. (M-type of *C. rubiginosa*), *Sellow* 1251 (B), 1393 (B-lectotype; LE).

Coccoloba acuminata HBK. Nov. Gen. 2: 176. 1817.

Coccoloba acuminata var. *pubescens* Lindau, Bot. Jahrb. 13: 193. 1890.

Coccoloba acuminata var. *glabra* Lindau, *ibid.* 194.

Coccoloba strobilulifera Meisner, Fl. Bras. 5(1): 25. 1855.

I discussed this species in an earlier paper (Jour. Arnold Arb. 40: 185. 1959) when I concluded that the amount of pubescence on the plant varied with the age and the vigor of the specimen. I cannot find any value or significance in the two varieties Lindau published.

A specimen from the Brazilian state of Pará, *Huber* 4393, bears an unpublished herbarium name attributed to Huber. The specimen is clearly referable to synonymy here.

A collection in the herbarium of the University of Wisconsin numbered "45" but without collector was supposedly made in La Lima, Chile. The authenticity is to be questioned as the specimen compares favorably with material from Colombia and Peru.

In addition to the specimens cited below, I have seen material from Guatemala, Honduras, Nicaragua, Costa Rica and Panama (Howard, *loc. cit.*).

Brazil. ACRE: Rio Macauhan, *Krukoff* 5666 (A, LE, M, NY). AMAZONAS: Rio Embira, *Krukoff* 4715 (A, LE, M, NY); Yuruá Miry, *Ule* 5723 (B). PARÁ: Pará, Alto Purus, Ponto Alegre, *Huber* 4393 (F, U). British Guiana. Courantyne, *Schomburgk* 1600 (B). Colombia. ANTIOQUIA: Río Magdalena, Brazuela de Perales, *Pennell* 3699 (GH). BOLÍVAR: San Martín de Loba, *Curran* 40 (GH), 100 (Y), 211 (Y). MAGDALENA: Río Magdalena near Mompós, *Humboldt* 1479

(Herb. Willd.-type of *C. acuminata*); Río Sevilla, *Record* 9 (A, GH, Y). SANTANDER: Río Magdalena, *Kalbreyer* 1280 (B). LOCALITY NOT SPECIFIED: *Goudot* 3 (B), *Moritz s.n.* (BR, LE, P-type of *C. strobilulifera* and *C. acuminata* var. *glabra*), *Triana s.n.* (B). Ecuador. Balao, *Eggers* 14239 (A, BR, LE, M). Peru. LORETO: lower Río Huallaga, *Llewelyn Williams* 4804 (A). Venezuela. YARACUY: Los Cañizos, plains of Yaracuy River, *Pittier* 8753 (GH). ZULIA: Perija, *Tejera* 253 (GH), *Mocquerys* 845 (P).

Coccoloba alagoensis Weddell, *Ann. Sci. Nat.* III. 13: 260. 1850.

Weddell based this species on *Gardner* 1389 from the state of Alagoas, Brazil. At present I am unable to determine the relationship of this species to *Coccoloba obtusifolia* Jacq. and *C. peruviana* Lindau. A full discussion will be found under *C. obtusifolia*.

Coccoloba alnifolia Casaretto, *Nov. Stirp. Bras.* 71. 1844.

Coccoloba populifolia Weddell, *Ann. Sci. Nat.* III. 13: 257. 1850; Meisner, *Fl. Bras.* 5(1): 40, *pl.* 18. 1855; Lindau, *Bot. Jahrb.* 13: 198. 1899.

Lindau accepted the Weddell name for this species, although he cited in synonymy the epithet Casaretto published several years earlier. Casaretto did not cite a specimen in the original publication, but it seems clear to me that the description and data given are based on his collection numbered 1194. This collection consists of two sheets in the Turino herbarium and I have designated one of them as the lectotype.

There is a possibility that the older epithet *Coccoloba firma* Martius ex Colla (1836) is the correct one for this species. The current difficulty in determining the type of *C. firma* will be discussed under that name.

Brazil. BAHIA: *Blanchet* 1486 (C, c-type collection of *C. populifolia*); *Sellow* 1137 (B), 793 (B). PERNAMBUCO: *Tapera*, *Pickel* 3681 (GH, NY). RIO DE JANEIRO: Tijuca, *Lützelburg* 343 (M); without specific locality, *Casaretto* 1270 (TO), *Gaudichaud* 420 (B, G, P), *Luschnath* 835 (LE), *s.n.* (M), *Martius s.n.* (M), *Riedel* 7 (BR, LE), 673 (LE, M), *Widgren* 719 (BR). STATE NOT SPECIFIED: Copacabana, *Casaretto* 1194 (TO-lectotype of *C. alnifolia*), *Nadeaud s.n.* (P). CULTIVATED: São Paulo Botanical Garden, *Hoehne* 28527 (A).

Coccoloba arborescens (Vellozo) Howard, *Jour. Arnold Arb.* 41: 44. 1960.

Polygonum arborescens Vellozo, *Flor. Flum.* 162. 1825, *Icones* 4: t. 43. 1827. *Coccoloba crescentiifolia* Chamisso, *Linnaea* 8: 134. 1833, "*crescentiaefolia*." *Coccoloba vellosiana* Casaretto, *Nov. Stirp. Bras.* 70. 1844. *Coccoloba fasciculata* Weddell, *Ann. Sci. Nat.* III. 13: 258. 1849. *Coccoloba crescentiifolia* var. *obtusata* Meisner, *Fl. Bras.* 5(1): 26. 1855.

The previous paper in this series (Howard, *loc. cit.*) contains a discussion of the nomenclature of this species. For the present, the type is considered to be the Vellozo illustration. After a careful study of this species in the field it may be desirable for some future monographer to select a modern specimen as neotype.

Brazil. BAHIA: *Blanchet 796* (F, NY, P-type of *C. fasciculata*). RIO DE JANEIRO: Praya Grande, *Sellow s.n.* (B, LE, M-type collection of *C. crescentiifolia*); *Glaziou 143* (BR); *Riedel 674* (A, BR, P). STA. CATARINA: Hooker Herb. without collector or number (K). STATE NOT SPECIFIED: Copacabana, *Luschnath s.n.* (BR); between San Juan and Rio dos Oistres, *Prince Maxim. Neuwied. s.n.* (BR, NY). LOCALITY NOT SPECIFIED: *Claussen 2013* (G, NY-type collection of *C. crescentiifolia* var. *obtusata*).

Coccoloba argentinensis Spegazzini, Physis 3: 176. 1917; Buchinger and Sanchez, Bol. Soc. Argent. Bot. 7: 251. 1959.

Coccoloba praecox Herter, Rev. Sudam. Bot. Montevideo 10: 38. 1952.

Spegazzini failed to select a type in the original description. He referred to material collected by M. Rigou in 1902 from the station "Mar-gherita," Prov. Santa Fe, and to material collected the following year in Reconquista. Correspondence with several Argentine botanists indicates that the Spegazzini herbarium has been neglected in the past and that some material has been lost. Dr. Maria Buchinger reported that she saw the "type" several years ago but currently there are no specimens of the species in the herbarium of Spegazzini at La Plata and no other herbarium contains such material. As long as there is a possibility that the original material may be located, a neotype should not be selected. In their recent paper Buchinger and Sanchez cite only one collection, *Schulz 240*, which I have not seen. They further consider the species to be endemic to the Chaco territory and to be found only in the provinces of Salta and Chaco, thereby eliminating the locality of the type collection.

The material cited below appears to me to correspond with the original description. *Coccoloba argentinensis* is easily recognized by the small obovate-elliptic leaves, the long fruiting pedicels, and the flowering of the plant before the leaves are fully developed.

Coccoloba praecox Herter was distinguished on these same characteristics but without comparison with the present species. I have examined an isotype and conclude that the reduction of *C. praecox* to the synonymy of *C. argentinensis* is necessary. *Coccoloba praecox* Herter is also a later homonym of *C. praecox* Wright ex Lindau (Bot. Jahrb. 13: 142. 1890).

Argentina. CHACO: Fontana, *Meyer 2517* (F); Las Palmas, *Jorgensen 2103* (GH, US), *2106* (GH); Resistencia, Colonia Benítez, *Petersen 3986* (A). JUJUY: Este Hacienda, s. of Jujuy, *Eyerdam & Beetle 22432* (GH). SALTA: Orán, Manuela Pedraza, *Eyerdam & Beetle 22647*, *22790* (G, GH); Pichanal, *Rodri-quez 1121* (GH, NY); Rosario de la Frontera, Los Baños, *Venturi 9402* (GH). TUCUMÁN: Capital, Barranca Colorada, *Venturi 955* (GH), *Schreiter 1516* (GH); Trancas, Tapia a Roca, *Schreiter* (Herb. Lillo 84971 (US), Vipos, *Venturi 9792* (A, GH, LE). Uruguay. Salto, Arapey, *Herter* (Herb. Herter 50852-type collection of *C. praecox*; F, P); Isla Gaspar, *Berro 3334* (G).

Coccoloba ascendens Duss ex Lindau, Bot. Jahrb. 13: 156. 1890.

In a previous discussion of this species (Jour. Arnold Arb. 40: 72, 73. 1959), I selected a specimen from Martinique, *Hahn 1005*, in the Berlin

herbarium as the lectotype. The species is well represented in the Lesser Antilles from Guadeloupe south to Trinidad. Lindau (Bot. Jahrb. 13: 156. 1890) cited specimens only from Guadeloupe, Martinique and Brazil. Eyma (Meded. Bot. Mus. Utrecht 4: 110. 1932) mentioned the distribution of the species as "Guyana, Brazil, Guadeloupe, Martinique." I have seen neither the specimens cited from the Guianas (*B.W.* 6560, 6600, and possibly *B.W.* 6490 and 6550b) nor those Lindau cited from the states of Pará and Goyaz in Brazil (*Burchell* 8034, 9345 and *Gardner* 3966). On the basis of an unnatural range I question particularly the Brazilian determinations given by Lindau. Future workers with additional material at their disposal doubtless will check the relationship of *Coccoloba ascendens* and *C. sparsifolia*.

***Coccoloba barbeyana* Lindau, Bot. Jahrb. 13: 185. 1890.**

I have examined the single collection cited by Lindau (*Ruiz & Pavon s.n.*, Peru, without definite locality, in the Barbey-Boissier herbarium) and failed to find the holotype or the species distinct in any way from *Coccoloba densifrons* Martius ex Meisner. Although Lindau accepted *C. densifrons* (based on a Martius collection from Ega in the Brazilian Amazon) he did not list the epithet in the key to the species.

***Coccoloba billbergii* Lindau, Bot. Jahrb. 13: 219. 1890.**

Lindau cited "*Coccoloba obtusifolia* Meissn. (non Jacq.)" in synonymy when he described *C. billbergii* based on *Billberg* 204 and 204a from Carthagera, implying that Meisner was in error. However, Meisner noted both the similarity of these Billberg collections to *C. obtusifolia*, as described and illustrated by Jacquin, and the discrepancy in the specimens so labeled in the Willdenow herbarium and the reference in the Willdenow catalogue. Lindau chose to interpret *C. obtusifolia* on the basis of the specimen in the Willdenow herbarium and incorrectly to consider *C. obtusifolia* as a species from the West Indies. I have examined the Billberg collections cited by Lindau from the Berlin and Stockholm herbaria. These are correctly associated with *C. obtusifolia* Jacq. as a South American species. *Coccoloba billbergii* Lindau must be considered a synonym of *C. obtusifolia* Jacq.

"*Coccoloba obtusifolia*" as used by Lindau (*loc. cit.* 146, 147) is correctly assigned to synonymy under *C. microstachya* Willd. (Howard, Jour. Arnold Arb. 38: 217-219. 1957).

***Coccoloba blanchetiana* Weddell, Ann. Sci. Nat. III. 13: 257. 1850.**

Weddell cited *Blanchet* 3561, from near Jacobina, Bahia, Brazil (c, p). This species is to be referred to the synonymy of *C. ochreolata* Weddell and will be discussed there.

Coccoloba bolivarana Llewelyn Williams, Trop. Woods 68: 39. 1941.

In a list of the forest trees of Venezuela, Williams refers to "Brusquillo Blanco, *Coccoloba bolivarana* (a new species), a tree about 8 m. high, growing in rocky areas, with a trunk ramified from the base, and bearing a juicy, lustrous black fruit." The species has not been published validly with a Latin description, to my knowledge, and the brief description given above is scarcely to be considered diagnostic in this difficult genus. Specimens in the herbaria of the Chicago Natural History Museum and the Royal Botanic Gardens, Kew, bear this name but attribute it to Standley. The specimens (*Williams 13374*) were collected at El Tigre, Los Garzones, on Río Cuchivero, Bolívar, Venezuela. They cannot be assigned to any recognized species and will be described in a later paper.

Coccoloba bracteolosa Meisner, Fl. Bras. 5(1): 30. 1855.

No type was selected in the original description, but a Martius collection without number from Joazeiro, on the Rio San Francisco, in Bahia, Brazil, has been photographed by other workers in the Munich herbarium and distributed as the type. I am referring this species to the synonymy of *Coccoloba ochreolata* Weddell and will discuss the problem under that name.

Coccoloba brasiliensis Nees & Martius, Nov. Act. Acad. Nat. Cur. 11: 30. 1823; Meisner, Fl. Bras. 5(1): 32. t. 13, f. 1. 1855.

Coccoloba senaei Lindau ex Glaziov, Bull. Soc. Bot. France 58: 571. 1911.

The original description cites first the locality of "X Valos" and then a general littoral distribution in Bahia, "Maragnanum" and Para, the latter attributed to Martius. I have seen no Martius specimens which fit the original description among the material from the Martius herbarium now at Brussels, Leningrad, or Munich. In his treatment of the genus for *Flora Brasiliensis*, Meisner redescribed the species and cited collections by Prince Maximilian and Martius. The illustration in *Flora Brasiliensis* is based on the specimen collected by Prince Maximilian and I select this as the lectotype.

A previous worker, possibly Meisner, has annotated some sheets to indicate a similarity to or a relationship with *Coccoloba rigida* Meisner. (Lindau, not following the homonym rule, accepted *C. parvifolia* Schott 1827, not Poiret 1804, and included in synonymy *C. rigida* Meisner.) Lindau distinguished between *C. brasiliensis* and "*C. parvifolia*" on the puberulent inflorescence axis in the latter species and the glabrous one in *C. brasiliensis*. An examination of the specimens cited below will show that the stem, ocreae, petioles, and frequently the base of the leaf blade are puberulent to short pilose in *C. brasiliensis*. The bracts and ocreolae of the inflorescence are likewise slightly puberulent to glabrous. On the characteristic of pubescence there is scant reason for separating *C. brasi-*

liensis and "*C. parvifolia*." However, the leaves of *C. brasiliensis* are variable in size and shape. In the type, and in the most recent collections, the leaves are thicker in texture and the bases are rounded-cordate, in contrast to those of "*C. parvifolia*." The inflorescence of the type is as compact as that of "*C. parvifolia*" but recent collections show longer, more lax inflorescences in which the ocreolae do not expand with the developing flower buds, and are, in fact, shorter than the bracts in all stages of development. Until these characteristics can be evaluated by field studies it seems desirable to retain *C. brasiliensis* as a species distinct from *C. rigida*.

The several sheets of the collections by Glaziou cited below suggest that the existing descriptions of *Coccoloba brasiliensis* are unsatisfactory and must be changed to accommodate the narrow, lanceolate-oblong leaves of the vigorous shoots and the large, oblong, but sessile, leaves of adventitious shoots. The Glaziou collection without number in the Paris herbarium has some leaves with blades 18 cm. long and 9 cm. wide. The largest leaf on the lectotype is 4 cm. long and 2.3 cm. wide, yet the collections cited below show all intermediates between these extremes.

The phrase "*Coccoloba senaei* Lindau n. sp." is used by Glaziou in a list of determinations of his collections. The brief description "Arbuste sarmenteux, fl. blanchâtres" can scarcely be considered diagnostic in this genus and I consider *C. senaei* to be a *nomen nudum*.

Brazil. MATO GROSSO: Barao de Capanema, Rio Cravary, *Baldwin* 3129 (US). MINAS GERAIS: Conselheiro Mata, *Brade* 13815 (B), 13816 (B); "in deserto Minarum," *Martius* s.n. (M); Rio dos Pedras, Valu, *Glaziou* 19762 (B, LE), 19763 (B, K, LE); Serra do Cipó, *Schwacke* 8005 (B), *Brade* 14841 (B). WITHOUT SPECIFIC LOCALITY: Valos, *Prince Maximilian* 88 (B, BR-lectotype; LE); *Glaziou* s.n. (P).

Coccoloba brasiliensis Sprengel, Syst. Veg. 2: 252. 1825.

This epithet is a later homonym of *Coccoloba brasiliensis* Nees & Martius. The species was based on a Sellow collection from Brazil which I have not seen. The description is not that of a species of *Coccoloba*. It was referred to the genus *Hedyosmum* of the Chloranthaceae by Chamisso (*Linnaea* 4: 36. 1833). I have not determined whether this is the same as *Hedyosmum brasiliense* Mart., recognized by Occhioni in his recent monograph of the genus (*Contribuição ao estudo de família Chloranthaceae com especial referencia ao gênero Hedyosmum* Sw. Rio de Janeiro, 1954).

Coccoloba candolleana Meisner, Fl. Bras. 5(1): 41. 1855.

Meisner based this species on the collection *Blanchet* 1818 from Bahia, Brazil. He noted its similarity to *Coccoloba cordata* Chamisso. I am unable to distinguish the two and so refer *C. candolleana* to the synonymy of the older name, *C. cordata*.

Lindau (Bot. Jahrb. 13: 201. 1890) cited *Goudot* 4, from Colombia, in

his treatment of *Coccoloba candolleana*. Several recent collections from Colombia have also been identified as this species. The Goudot specimen in the Berlin herbarium cited by Lindau is a fragment of a larger specimen in the Paris herbarium. A study of the latter sheet clearly indicates that this collection is to be referred to *C. padiformis* Meisner, the type of which is from Caracas, Venezuela.

***Coccoloba caracasana* Meisner, DC. Prodr. 14: 157. 1856; Howard, Jour. Arnold Arb. 40: 193. 1959.**

Coccoloba caracasana f. *glabra* Lindau, Bot. Jahrb. 13: 211. 1890.

Coccoloba cyclophylla Blake, Contr. U.S. Natl. Herb. 20: 238. 1919.

In an earlier paper I discussed the significance of pubescence in this species and cited the collections seen from Mexico and Central America. *Coccoloba cyclophylla* Blake is now added to the synonymy of this species. Blake compared his species, based on *Curran* 47, from Colombia, with one from Hispaniola and concluded that they were distinct. A proper comparison would have been with *C. caracasana* from Venezuela, which is clearly the same.

Colombia. ATLÁNTICO: La Plaza, Juan Mina, *Dugand* 643 (Y); Molinero, *Dugand* 568 (Y). BOLÍVAR: Castillo Maldonado, *Sessé & Mociño* 5430 (F); San Martín de Loba, *Curran* 47 (US-type of *C. cyclophylla*; GH, Y). Magdalena, Santa Marta, *Smith* 1702 (A, GH); Tucurínca, *Romero* 1388 (US). LOCALITY NOT KNOWN: *Moritz* 1109 (BR, LE). **Venezuela.** APURE: San Fernando de Apure, *Grisol s.n.* (A, P). ARAGUA: Maracay, *Vögl* 1009 (M); San Juan de los Morros, *Alston* 6023 (BM). CARABOBO: Between San Joaquín and Mariara, *Pittier* 12111, 12112 (G, LE, M); Valencia, *Pittier* 8705 (GH). DISTRITO FEDERAL: Caracas, *Vargas* 30 (G); *Humboldt* 732 (Herb. Willd.); *Bonpland* 732 (B-holotype). GUARICO: El Sombrero, *Pittier* 11460 (A, G, GH, M), 12367 (M, NY); La Rubiera, *Pittier* 12328 (G, M). LARA: Between Yaritagua and Duaca, *Pittier* 343 (A, M). MERIDA: Tovar, *Fendler* 2053 (GH). YARACUY: Bruzual, *Curran* 642 (NY).

***Coccoloba carinata* Ruiz ex Meisner, DC. Prodr. 14: 150. 1856.**

Meisner published this epithet in synonymy under *Muehlenbeckia leptobotrys* Meisner and stated that it was a manuscript name found in the herbarium at Berlin. I have not seen authentic material.

***Coccoloba caurana* Standley, Field Mus. Publ. Bot. 22: 73. 1940; L. Williams, Explor. Bot. Venez. 189. 1942.**

Although the description of this species was published twice as new, the taxon belongs in the synonymy of *Coccoloba fallax* Lindau and is discussed in more detail under that name. The type, in the herbarium of the Chicago Natural History Museum, is *Williams* 11366, from Venezuela.

Coccoloba cerifera Schwacke, Pl. Nov. Mineir. 1: 7. 1898.

I have not seen the original publication to check the validity of this name and so, for the present, must interpret the species from the specimen indicated as the type in the Berlin herbarium. The plant is unlike any other species found in southern Brazil. It resembles *Coccoloba schomburgkii* in the shape and thickness of the leaves, but differs from it in having long pedicels from which the apparently staminate flowers have fallen. The Pires and Black collection cited below compares well with the type specimen.

Brazil. MINAS GERAIS: Serra do Cipó, *Schwacke 11780* (B-holotype), *Pires & Black 2816* (NY).

Coccoloba charitostachya Standley in A. C. Smith, Lloydia 2: 176. 1939.

The type of this species is *A. C. Smith 2356*, collected near the mouth of the Charwair Creek, in the basin of the Rupununi River, British Guiana. The holotype is in the herbarium of the Chicago Natural History Museum.

This species is not well defined in the original description and has not been recollected. Additional material is badly needed for an understanding of the species. At present the species may be characterized by the slightly rugose leaf blades which are elliptic-ovate in shape, rounded at the apex and lighter in color on the lower surface. The fruits are all insect-infested and abnormal and of no diagnostic value. Flowers are not known.

Coccoloba chacoensis Standley, Field Mus. Publ. Bot. 17: 239. 1937.

This species is to be referred to the synonymy of *Coccoloba spinescens*. *Coccoloba chacoensis* was based on *Cardenas 2529*, from Bolivia; the holotype is in the Chicago Natural History Museum. Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 253. 1959) recognized this species and maintained it as distinct from *C. spinescens* Morong because of the absence of lateral branches terminating in spines and the presence of "glands" on the lower leaf surface. Although the Argentine botanists undoubtedly know these species in the field, the characteristics they have chosen to separate the species are not reliable in herbarium specimens. The holotype compares favorably with such collections as *Morong 882* (the type of *C. spinescens*) and *Hassler 11476* and *2486*.

Coccoloba confusa Howard, nom. nov.

Coccoloba declinata Martius, Beibl. Flora 20: 90. 1837; Meisner, Fl. Bras. 5(1): 29. 1855, as to plants, not as to name.

Coccoloba declinata var. *major* Meisner, Fl. Bras. 5(1): 30. 1855.

Coccoloba declinata var. *minor* Meisner, *ibid*.

Polygonum declinatum Vellozo (Flor. Flum. 162. 1825, Icon. 4: t. 41. 1827) was described briefly and in general terms. The illustration given

in the *Icones* is a poor one showing scarcely any characteristic of value in defining the taxa in *Coccoloba*. It was suggested by Dr. I. M. Johnston in his library notes that Pharmacopolis, the locality given, might be near the mouth of the Rio Taquari in the western part of the state of Rio near Paraty.

The transfer of the Vellozo name to *Coccoloba* made by Martius in an obscure paper is seldom correctly cited. Martius refers to two specimens, one from "Montem Talegraphi," in "Prov. Sebastianopolitana," and the other near Pendamonhangaba and Taubaté, in São Paulo. Martius' brief description of *Coccoloba declinata* is obviously based on the specimens cited and could scarcely be drawn from either the description or the plate given by Vellozo.

In 1855 when Meisner prepared the treatment of the genus for the *Flora Brasiliensis*, he described the species and established three new varieties: α *minor*, β *Velloziana* and γ *major*. For *Coccoloba declinata* var. *minor*, Meisner cited in reference "*Coccoloba declinata* Mart. Herb. propr." and a specimen from the Rio Doce collected April 1816 by Prince Maximilian. I have not seen this specimen in material from Brussels, Leningrad, Munich, or New York, the usual places for Martius and Meisner specimens. Meisner's variety, *Velloziana*, is based on the epithet and reference "*Polygonum declinatum* Vellozo Flor. Flum. IV. t. 41" and in place of a specimen Meisner cites "in prov. Rio de Janeiro."

Neither Meisner nor more recent authors cite the specimen from "Montem Talegraphi" which Martius mentioned in the original transfer of the Vellozo name. The specimen from Pendamonhangaba is referred by Meisner to his var. *major*.

Meisner prepared the treatment for *Coccoloba* in DeCandolle's *Prodramus*, using the same broad concept of varieties comprising the species *C. declinata*. In this treatment, however, the assignment of var. *major* to the species is questioned.

In his monograph of the genus Lindau reduced to synonymy Meisner's varieties *minor* and *Velloziana*. Lindau recognized the var. *major*, but commented on the poor condition of the type specimen and suggested that it might be a new species.

There appear to be no Vellozo collections available; thus the interpretation of the species must be made from the inadequate original description and the rather poor drawing. In comparing the drawing with the specimens cited by Martius, Meisner and Lindau, I am convinced that these authors have misinterpreted Vellozo's species. Vellozo's drawing shows that a scrambling plant is intended, but the material cited by previous authors for *Coccoloba declinata* is shrubby, with geniculate branches. Again, the drawing shows a short, regular inflorescence, while the young inflorescences of the specimens cited by earlier authors are geniculate, with the older inflorescences elongate. The most obvious match for the Vellozo species is the Martius specimen cited as the type of *C. racemulosa*. This is a liana with short lateral branches and comparable

inflorescences. The venation of the type of *C. racemulosa* compares favorably with that illustrated by Vellozo, while the venation of specimens cited by Martius, Meisner and Lindau does not. It appears to me that the drawing of *Polygonum declinatum* Vellozo most nearly compares to *Coccoloba racemulosa* Meisner.

The material which Martius, Meisner and Lindau cited and described as *Coccoloba declinata* therefore requires a new name. I propose the name *C. confusa*, to call attention to this problem. Lindau's description (Bot. Jahrb. 13: 166. 1890) applies to the specimens cited, including those originally mentioned by Martius in transferring Vellozo's specific epithet.

The inclusion of the Krukoff and the Archer collections from Amazonas and Pará creates a sizeable gap in the known range of this species. On the basis of available material, these specimens must be assigned here.

Brazil. AMAZONAS: Humaytá near Livramento, *Krukoff* 6669 (NY). PARÁ: Belém, *Archer* 7830 (F, K). RIO DE JANEIRO: Caju, *Riedel s.n.* (LE); Copacabana, *Luschnath s.n.* (LE); Rio de Janeiro, *Glaziou* 3089 (BR), *Riedel* 675 (A, BR, LE, M), 676 (A, BR, LE, M); Telegraphenberg, *Luschnath*, Oct. 1833 (BR). SÃO PAULO: Pedamhongaba, Taubaté, *Martius* "66" (BR, LE, M-type of *C. declinata* var. *major*).

Coccoloba conduplicata Maguire, Bull. Torrey Bot. Club 75: 304. 1948.

A clear-cut species, but known only from the material cited in the original description. The folded leaf blade noted in the specific name appears to be of less significance than the author indicates, since the majority of the leaves are not conduplicate.

Surinam. Tafelberg, *Maquire* 24437 (A, BR; NY-holotype), 27205 (A, NY).

Coccoloba cordata Chamisso, Linnaea 8: 133. 1833.

Coccoloba candolleana Meisner, Fl. Bras. 5(1): 41. 1855.

Coccoloba cordata var. *praecox* Hassler, Repert. Nov. Sp. 14: 162. 1915.

Both Meisner and Lindau have indicated the similarity of *Coccoloba cordata* Chamisso and *C. candolleana* Meisner. Lindau distinguished between these in his key by placing *C. candolleana* in a group of species having leaves glabrous on both surfaces and *C. cordata* in one having leaves pubescent along the midrib and nerves on the lower surface. Lindau has placed the two species adjacent to one another in the text. Among the major characters of these species, Lindau described *C. candolleana* as having tomentose ocreae while those of *C. cordata* are glabrous.

The type collection of *Coccoloba cordata* is *Sellow s.n.* from the Rio Pardo area of Brazil. I have seen three sheets of this collection. One in the herbarium at Berlin bears the full data given by Chamisso and is selected as the lectotype. The other two were annotated only "*C. cordata* N."

The descriptions given by Chamisso and Lindau are not entirely accu-

rate. Various branches of the specimens comprising the type collection have puberulent or tomentose ocreae, although other portions are glabrous. Most of the leaves are coarsely pubescent along the midrib at the base of the leaf, but some are completely glabrous.

Coccoloba candolleana was based on *Blanchet 1818*. A single specimen is cited as being at Geneva while a smaller specimen from the Meisner herbarium, now at the New York Botanical Garden, bears several of Meisner's annotations: (1) "*C. cordata* Cham. ?" which he declared to be different on the basis of the shorter petiole and more coriaceous blades; (2) a variety of *C. cordata* named for Blanchet, a name which was not published, and finally (3) "*Coccoloba candolleana* n." The Blanchet collection has broader leaves and shorter petioles, but can be compared favorably with portions of the Sellow collection which is the type of *C. cordata*.

In his monograph Lindau included a collection from Colombia (*Goudot 4*) in the description of *Coccoloba candolleana*. This collection is better referred to *C. padiformis*, a species known from Venezuela and Central America (Howard, Jour. Arnold Arb. 40: 210. 1959).

Coccoloba cordata var. *praecox* Hassler was based on a specimen, *Hassler 7279*, from Paraguay which is staminate, in contrast to the pistillate type of *C. cordata*. The deciduous characteristic of the plant is not significant, and the variety is not worthy of recognition.

Argentina. CHACO: Barranqueras, Isla de Temores, *Curran 402* (US). FORMOSA: Comán, *Jørgensen 2064* (GH, US); Pirané, *Morel 432* (BR). JUJUY: San Pedro, *Di Lella and Garcia 2820* (A). MISIONES: Apóstoles on Río Chimiray, *Ibarrola 1150* (V). SALTA: Embaracación, *Eyerdam & Beetle 22916, 22928* (GH); Orán, Tabacal, *Schreiter 5472, 8455* (GH); Orán, Vespució a las Hablillas, *Schreiter 11492* (F); Río Blanco, *Venturi 5585* (F, GH, LE, M); Río Piedras, *Rodríguez 73* (F). TUCUMÁN: Capital, Barranca Colorada, *Venturi 955* (F); Raco, *Schreiter 1516, 8443* (GH). **Brazil.** BAHIA: *Blanchet 1818* (G, NY-type collection of *C. candolleana*). RIO GRANDE DO SUL: Rio Pardo, *Sellow s.n.* (B-lectotype; M). SÃO PAULO: *Gaudichaud 140* (P). **Paraguay.** CHACO: Villa Rica, *Balansa 3277* (G). Concepción, *Hassler 7279* (GH-type of *C. cordata* var. *praecox*).

***Coccoloba cordifolia* Meisner, Fl. Bras. 5(1): 37. 1855.**

Meisner cited several specimens but did not indicate a type. A sheet in the Delessert herbarium has been cited as the type by previous workers, although it bears two branches and two labels (*Blanchet 100* and *Blanchet 3528*). Meisner (DC. Prodr. 15: 155. 1856) suggested that *Coccoloba laevis* might be identical with *C. cordifolia*. Lindau (Bot. Jahrb. 13: 186. 1890) combined the two, accepting the older *C. laevis* Casaretto, a step which I believe to be correct.

***Coccoloba coronata* Jacquin, Enum. Pl. Carib. 19. 1760, Select. Stirp. Am. Hist. 114. t. 77. 1763; Dugand, Caldasia 4: 427. 1947; Howard, Jour. Arnold Arb. 41: 40. 1960, not Lindau, Symb. Ant. 1: 228. 1899.**

Coccoloba virens Lindley, Bot. Reg. 21: t. 1816. 1835.

Coccoloba novogranatensis Lindau, Bot. Jahrb. 13: 192. 1890; Howard, Jour. Arnold Arb. 40: 85-87, 208, 209. 1959.

Coccoloba dioica Karsten ex Lindau, Bot. Jahrb. 13: 170. 1890.

Coccoloba caribaea Urban, Symb. Ant. 5: 337. 1907.

Coccoloba waittii Johnston, Sargentia 8: 122. 1949.

The correct name of this species has evolved through the series of my papers cited above with the final correction suggested by one of Dugand's papers which I had overlooked. It is possible that *Coccoloba jagifolia* Jacq. should be assigned to the synonymy of this species as well. The identity of that plant will be discussed under that epithet.

I have not seen any material collected by Jacquin, and the species is regarded as typified by an illustration. Specimens from St. Vincent, south to Trinidad and Tobago, and from Guatemala and Panama are cited in earlier papers (Jour. Arnold Arb. 40: 85, 209. 1959). I have also examined the following specimens from South America.

Colombia. BOYACÁ: Between Anapoima & Apulo, *Triana* 978 (B, P-type of *C. novogranatensis*); El Humbo, *Laurance* 760 (A); Santa Marta, *H. H. Smith* 2421 (A, BR). BOLIVAR: Sabanilla, *Karsten s.n.* (B, LE). CAQUETÁ: Hetuchá on Río Ortegua, *Woronow & Juzepczuk* 6100 (F). MAGDALENA: Molino, *Haught* 4148 (F, NY). DEPT. NOT KNOWN: Pozo del Higuierón, *Usiacuri*, *Dugand* 788 (Y). **Ecuador.** El Oro, Arenillas, *Little* 6721 (F). **Peru.** LORETO: Río Putumayo, *Klug* 2240 (A, B, GH). **Venezuela.** ANZOATEGUI: Soledad, *Gines* 3913 (US). BOLÍVAR: Between Upata & Altagracia, *Steyermark* 57681 (F). DISTRITO FEDERAL: Barrancas, *Tamayo* 1315 (US); Caracas, *Karsten s.n.* (LE—holotype of *C. dioica*). SUCRE: Cristóbal Colón, *Broadway* 143, 144, 491 (GH, NY, US). ZULIA: Perija, *Tejera* 91 (US). DEPT. NOT KNOWN: Sta. Ana, Paraguana, *Tamayo* 854 (US).

Coccoloba corrientina Rojas, Bull. Geogr. Bot. 28: 162. 1918.

The original description of this species is brief and generalized. No specimens are cited and, in fact, a broad general distribution is attributed to the species. Through personal correspondence I have learned from Dr. Maria Buchinger and other Argentine botanists that no Rojas collections can be attributed to this species. The species appears to be impossible to typify.

Buchinger and Sanchez (Bol. Soc. Argent. Bot. 7: 255. 1959) list *Coccoloba corrientina* as a questionable species, but suggest its similarity to *C. morongii*, the correct name of which is *C. paraguariensis*. I concur with this suggestion.

Coccoloba crescentiifolia Chamisso, Linnaea 8: 134-136. 1833, "*crescentiaefolia*."

The correct name of this species is *Coccoloba arborescens* (Vellozo) Howard based on *Polygonum arborescens* Vellozo. For a discussion of the nomenclature and additional synonymy see the previous paper in this

series (Jour. Arnold Arb. 41: 43-45. 1960). Specimens previously referred to this species are listed under *C. arborescens* above.

Coccoloba cruegeri Lindau, Bot. Jahrb. 13: 209. 1890.

Coccoloba ernstii Johnston, Proc. Am. Acad. 40: 685. 1905.

Coccoloba oblonga Lindau, Bot. Jahrb. 13: 136. 1890.

This species was based on a Crueger collection from Trinidad. Lindau described the fruits and assigned the species to the section *Campderia*. Currently available collections from Berlin and Göttingen are fragmentary and sterile. The specimen from the Trinidad herbarium appears to have had flowering parts at one time. There is some doubt as to what Lindau actually saw and described, for there is no evidence in the vegetative parts that the species is related to the others which he assigned to section *Campderia*.

Coccoloba oblonga Lindau was described at the same time as *C. cruegeri* and was based on *Riedel 614*, reported to be in "herb. Petrop." I have now seen that specimen and the others cited below, and there is no question that *C. oblonga* is the same as *C. cruegeri*. The Riedel collection from Ilheos, Bahia, represents a sizeable, but not unlikely, extension of range. As Lindau indicated, the material is for all practical purposes sterile, although the specimens do have immature and poorly preserved inflorescences and flowers.

The range of this species is now from the islands of Trinidad and Margarita to British Guiana and Bahia in Brazil. Collections from Trinidad and Margarita were cited in an earlier paper (Jour. Arnold Arb. 40: 75, 76. 1959).

British Guiana. Ituribisi Lake, Essequibo Coast, *Forest Dept. B.G. 5474* (A, K). **Brazil.** BAHIA: Ilheos, *Riedel 614* (B, LE, P-type of *C. oblonga*); without specific location, *Blanchet 3160A* (P). **Venezuela.** SUCRE: Cristóbal Colón, *Broadway 697* (GH).

Coccoloba cujabensis Weddell, Ann. Sci. Nat. III. 13: 259. 1850.

Coccoloba longiochreata Hassler, Repert. Spec. Nov. Reg. Veg. 14: 162. 1915.

One specimen of *Martius 1241* in the Munich herbarium has been designated as the lectotype of this species. *Coccoloba cujabensis* is suggestive of *C. ruiziana* Lindau, but field study or additional collections are necessary to determine their correct relationship.

Hassler compared his new species, *Coccoloba longiochreata*, with *C. alagoensis* Weddell and *C. floribunda* Lindau. He distinguished it on the basis of the larger ocreae. The type selected by Hassler is a vigorous staminate flowering specimen. The type of *C. cujabensis* is a fruiting collection. On the basis of vegetative characteristics they are similar, and any question is resolved by a study of the Werdermann and Kuntze collections cited below. These show the intermediate conditions of ocreae and leaf venation between the type specimens of *C. cujabensis* and *C.*

longiochreata. *Coccoloba cujabensis* is not at all comparable to *C. alagoensis* or "*C. floribunda*."

Bolivia. Beni, Trinidad, Misiones Guarayos, *Werdermann* 2366 (MO). **Brazil.** MATO GROSSO: Corumbá, *Kuntze s.n.* (NY); Cuyabá at Patricio da Silva Manso, *Martius* 1241 (B, BR, LE; M-lectotype). **Paraguay.** Chaco, *Fiebrig* 1284 (M-type collection of *C. longiochreata*).

Coccoloba cyclophylla Blake, *Contr. U. S. Natl. Herb.* 20: 238. 1919.

The type is *Curran* 47, from San Martín de Loba, Dept. Bolívar, Colombia (US 537207). Blake compared his new species with "*Coccoloba rotundifolia* Meisner," now known as *Coccoloba leoganensis* Jacq., from Hispaniola. There is no question that *C. cyclophylla* is the same as *C. caracasana* Meisner, which was based on material from Caracas, Venezuela.

Coccoloba cylindrostachya Lindau, *Bot. Jahrb.* 13: 163. 1890.

Lindau described consecutively *Coccoloba cylindrostachya* (based on *Glaziou* 13135) and *C. glaziovii* (based on *Glaziou* 8089) in his monograph of the genus. Both collections were made in the vicinity of Rio de Janeiro. An examination of the specimens fails to support the differences which Lindau felt would separate the two species. Therefore, *C. cylindrostachya* has been referred to the synonymy of *C. glaziovii*.

[To be continued]

